ANNALS
OF THE
ENTOMOLOGICAL SOCIETY
OF AMERICA

Volume 53 November, 1960 Number 6

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Published by the

ENTOMOLOGICAL SOCIETY OF AMERICA

R. H. NELSON, *Executive Secretary*
4603 Calvert Road,
College Park, Maryland

ROLAND F. HUSSEY, *Editor*
Department of Biology
University of Florida,
Gainesville, Florida

F. W. POOS, *Managing Editor*
4603 Calvert Road
College Park, Maryland

EDITORIAL BOARD

L. E. ROZEBOOM, *Chairman*, Baltimore, Md. (D, 1960)
J. A. ADAMS, Poughkeepsie, N. Y. (C, 1961)
J. J. PRATT, Wayland, Mass. (B, 1962)
F. N. YOUNG, Bloomington, Ind. (A, 1963)
P. D. HURD, Berkeley, Calif. (A, 1964)

A bimonthly journal published on the 15th of January, March, May, July, September, November, devoted to the interest of classical entomology. Authors are entirely responsible for statements in the *Annals*, whether of fact or opinion.

TERMS OF SUBSCRIPTION. Non-members in North America and U. S. Possessions—$15.00 per year; elsewhere—$15.00 plus 60¢ postage. Single copies $3.00. **Deliveries overseas** are not guaranteed and foreign mailings are made at the subscriber's risk.

A *single order* for the Annals of the Entomological Society of America and the Journal of Economic Entomology, *if sent to the same address*, may be obtained at a **COMBINATION PRICE** of $27.00 per year, domestic; $28.20 foreign.

LOST NUMBERS. Missing numbers cannot be supplied free of charge unless notice is received within 60 days after the appearance of issues concerned.

BACK NUMBERS. The Executive Secretary will be glad to quote prices upon request.

REPRINTS. No gratis copies are supplied. A schedule of prices which will apply to orders received before the Annals is printed, and an order form are sent with proof. For price schedule, see Bulletin of the Entomological Society of America, Vol. 5(2):86, June, 1959, or page 509 of Vol. 49(5) of the *Annals*.

BUSINESS COMMUNICATIONS of the Society and **SUBSCRIPTIONS AND MATTERS PERTAINING TO ADVERTISEMENTS** should be sent to the Executive Secretary, Entomological Society of America, 4603 Calvert Road, College Park, Md. Changes of address must reach the office of the Executive Secretary 5 days prior to the month of issue to be effective for that month. Members should make use of the postal regulations which provide for forwarding of second class mail if postage upon delivery is guaranteed.

ALL MANUSCRIPTS and other copy for the *Annals* should be sent to the Executive Secretary. Prompt publication of acceptable matter may be secured by payment of the cost of printing and engraving ($18.00 per page plus cost of engravings with additional charge for excessive tabular matter). Cost of engravings in excess of $20.00 for each eight printed pages or major fraction thereof, will be charged to the author. Before preparing manuscripts for publication in the *Annals*, authors are urged to consult the Publication Policies and Manuscript Rules and Suggestions given in Vol 49(5): 506–9, September 1956.

Second class postage paid at Columbus, Ohio. By order of Dec. 10, 1958.

Printed by The Spahr & Glenn Company,
50 East Broad Street
Columbus 15, Ohio, U. S. A.

Issued December 21, 1960

Annals of
The Entomological Society of America

Volume 53 NOVEMBER, 1960 No. 6

THE IMPORTANCE OF TAXONOMY TO BIOLOGICAL CONTROL AS ILLUSTRATED BY THE CRYPTIC HISTORY OF APHYTIS HOLOXANTHUS N. SP. (HYMENOPTERA: APHELINIDAE), A PARASITE OF CHRYSOMPHALUS AONIDUM, AND APHYTIS COHENI N. SP., A PARASITE OF AONIDIELLA AURANTII[1]

PAUL DeBACH[2]

Department of Biological Control, University of California Citrus Experiment Station, Riverside

ABSTRACT

Past misidentification of *Aphytis holoxanthus* n. sp. as *Aphytis lingnanensis* Comp. retarded its use and distribution in various countries for the biological control of *Chrysomphalus aonidum* (L.). To a lesser degree the same applies also to *Aphytis coheni* n. sp., a parasite on *Aonidiella aurantii* (Mask.) in Israel, which was thought to be *Aphytis lingnanensis*. The correct identification makes an additional parasite species available for testing in biological control attempts against *Aonidiella aurantii*. *Aphytis holoxanthus* and *Aphytis coheni* are described as new species. A key separating them from other similar-appearing species is given.

HISTORY

The first species to be described herein as new, *Aphytis holoxanthus* (Hymenoptera: Aphelinidae), has been hidden for the past 12 years or so by the common assumption that it was *A. lingnanensis* Comp. The second new species, *A. coheni*, has for the past few years also been referred to as *A. lingnanensis* and has not been distinguished from *A. holoxanthus*, with which it occurs in Israel.

It all began in November 1947 when *Aphytis lingnanensis* (then undescribed) was obtained in Riverside from a shipment of Florida red scale material (*Chrysomphalus aonidum* (L.)) imported from South China. Flanders (1953) listed the host of *Aphytis lingnanensis* as *C. aonidum* but cultured it on the California red scale, *Aonidiella aurantii* (Mask.), in the insectary. During 1948 it was first colonized in the field in California against the California red scale. Subsequently it became well established in many areas at the expense of the previously established *Aphytis chrysomphali* (Mercet) (De Bach and Sisojević 1960). At that time *Aphytis lingnanensis* was assumed to be a species adapted to more than one host species, which is not at all unusual.

The first doubt arose when the author, in December 1948, found *Aphytis lingnanensis* already accidentally well established and widespread in the Rio Grande Valley of Texas. Surprisingly, though, it was vigorously attacking *Aonidiella aurantii* but not *Chrysomphalus aonidum* (except for occasional male scales) even when both scales occurred on the same citrus trees.

Subsequently, I posed the question to my colleagues, S. E. Flanders and H. Compere, whether the original stock of *Aphytis lingnanensis* imported into California from South China might have come from *Aonidiella aurantii* rather than from *Chrysomphalus aonidum*. There was no evidence in the original Sender's and Receiver's (S. & R.) Report to indicate this, although the possibility remained that *Aonidiella aurantii* had been mixed in with the predominant *C. aonidum*. Compere (1955) described the species as *Aphytis lingnanensis*; it had previously been designated *Aphytis* "A".

The same question arose—but this time more emphatically—in connection with the author's 7-month study of parasites of diaspine scales in Mexico in 1954. *Aphytis lingnanensis* was found to be common and well distributed throughout the citrus areas of Mexico. It is the principal parasite of *Aonidiella aurantii* in that country and was found commonly attacking several other species of scales as well, but, as in Texas, *Aphytis lingnanensis* was not discovered attacking any stages of

[1]Paper No. 1224, University of California Citrus Experiment Station, Riverside, California. Accepted for publication July 30, 1960. Partial cost of publication of this paper was met by the Citrus Experiment Station, Department of Biological Control, Riverside, California.

[2]Thanks are due to E. B. White and S. C. Warner, who performed the interspecific hybridization tests reported herein, as well as various biological evaluation tests, and who maintained the cultures.

the female *Chrysomphalus aonidum* and only rarely the male scales. At that time I was inclined to believe that either the Mexican *C. aonidum* was actually a different species or strain or the Mexican *Aphytis lingnanensis* was different. However, H. L. McKenzie and R. C. Dickson (personal communication) subsequently identified the scale definitely as *C. aonidum*, and the *Aphytis lingnanensis* was proved conspecific with the California (South China) form in our laboratory by crossing tests in which they freely hybridized.

Because of the situation in Mexico, when E. Jiménez J., Oficina de Control Biológico, Dirección General de Defensa Agrícola, México, D. F., wrote us in March 1955 requesting possible parasites of *Chrysomphalus aonidum* from California, I answered ". . . we do not have any parasites here which we know will attack this scale. . . ." even though *Aphytis lingnanensis* in California was recorded as coming from *C. aonidum* in China but which, as already mentioned, the evidence from Texas and Mexico contradicted.

For the same and other reasons, when I. Cohen, of the Citrus Marketing Board in Israel, wrote in July and August 1955 to my colleagues, H. Compere and S. E. Flanders, and to me regarding sources of possible parasites of *Chrysomphalus aonidum* for use in Israel, we suggested principally importing *Casca smithi* Compere from Hong Kong and *Prospaltella aurantii* (How.) from Florida. I did not suggest importing *Aphytis lingnanensis* from Hong Kong for the reasons already given. Flanders stressed the importation first of *Casca smithi* from Hong Kong (which he considered to be the key parasite) and subsequently of *A. "lingnanensis"* which he had observed in 1954 to be a common parasite of *Chrysomphalus aonidum* there. As it turned out, shipments in 1956 from Hong Kong yielded predominantly *A. "lingnanensis,"* and Cohen decided to go ahead and colonize it since *Casca* was very scarce and not amenable to culture. This was a fortunate decision inasmuch as *A. "lingnanensis,"* later described herein as *A. holoxanthus*, produced complete biological control within 2 to 3 years.

Meanwhile, in December 1956, the author visited Hong Kong and other Oriental areas and observed what was considered to be *Aphytis lingnanensis* as the dominant parasite of *Chrysomphalus aonidum*. This opinion was based on identification of large numbers of field-collected pupae which were of the typical lingnanensis type (DeBach 1959). Thus, I came to believe that *Aphytis lingnanensis* was, after all, a principal parasite of *C. aonidum* as well as of *Aonidiella aurantii*. After returning from the Orient, I wrote E. Malkiely in Israel in November 1957 as follows: "I saw *Aphytis lingnanensis* on Florida red scale most commonly in the Orient, but I am also quite sure that one or more other species of *Aphytis* were common in certain areas. In general, Florida red scale is quite scarce throughout the various citrus-growing areas I visited in the Orient, and the observational evidence indicates that natural enemies were responsible. My opinion is that *Aphytis lingnanensis* may be capable of efficient control of Florida red scale by itself. . . . This species also attacks the California red scale."

Also, in writing to I. Cohen in December 1957, the author said, "I was very much interested in your comments on the excellent progress of *Aphytis lingnanensis* on Florida red scale in Israel. It may be also that its work on the California red scale will be more satisfactory than in California because in your case you have the two species of scales as hosts and the Florida red scale does not have the disadvantage of nonsusceptible stages which should insure a regular production of parasites in the field."

The author's subsequent thinking on this problem was summarized in a July 1958 letter to H. A. Dean, of the Lower Rio Grande Valley Experiment Station, Weslaco, Texas, in response to a query regarding importation of parasites of *Chrysomphalus aonidum* into Texas:

"Regarding parasites of Florida red scale, I don't think we have anything here [in California] that would be of help to you. However, as you may know, we suggested to Israeli entomologists several years ago that they obtain *Aphytis lingnanensis* from Hong Kong where it is common on the Florida red scale. They have done this and report very good progress to date. It is quite possible that the *lingnanensis* they have represents a Florida red scale strain which would differ from the one you already have in Texas on California red scale. If this is not the case, then perhaps your Florida red scale and that of Mexico differ from that in the Orient and in Israel. In Mexico, where *Aphytis lingnanensis* is common and generally distributed, it practically never attacks the large female of Florida red scale [as it does in Israel].

"Perhaps you and Don Clancy [of the U. S. Department of Agriculture and stationed in Florida] could get together and arrange for parasites to be sent from Israel."

The U. S. Department of Agriculture subsequently obtained a stock of the Florida red scale *Aphytis* from Israel early in 1959. Cultures then were sent by D. W. Jones of the U. S. Department of Agriculture Parasite Introduction Laboratory at Moorestown, New Jersey, to Clancy in Florida and Dean in Texas for field colonization, and to the author in California for taxonomic and biological studies. Culture in our laboratory was necessarily on a factitious host (principally *Aspidiotus hederae* (Vallot)) because *Chrysomphalus aonidum* is not established in California. The parasite, however, was easily cultured on this host species and as soon as sufficient numbers were available, study and tests were begun.

Because we have come to realize that several species of *Aphytis* may be masquerading under one name (Compere 1955; DeBach 1959), it has become our policy to attempt crosses between any new importation and other similar-appearing species cultures in stock. Therefore, one of the first procedures was to attempt to cross—in reciprocal crosses—specimens from the Israeli Florida red scale culture with specimens of *A. lingnanensis* (of Oriental origin), of *A. fisheri* DeBach, and of *A. melinus* DeBach. No hybrid progeny whatsoever resulted. Early in 1960, additional shipments from Israel direct to California of the Israeli Florida red scale *Aphytis* gave a culture which crossed readily with the one obtained in 1959 from Israel via the U. S. Department of Agriculture, hence giving us a double check on the host record. Meanwhile, microscopic study of specimens mounted on slides showed characters that were consistently and definitely distinct from *A. lingnanensis* or other described species. No doubt remained that the Israeli Florida red scale *Aphytis* was a new species. It is described under the name *Aphytis holoxanthus* later in this paper.

Had this species, *Aphytis holoxanthus*, been recognized as new and as a parasite of *Chrysomphalus aonidum* when it undoubtedly was received in California in 1947–48 in shipments of *C. aonidum* from South China, it would have been available years earlier than it was for use in biological control of *C. aonidum* in many citrus-growing countries. This is an outstanding illustration of the need for and importance of accurate taxonomic study to practical biological control.

Why was this species thought to be *Aphytis lingnanensis* for so long? The first source of confusion occurred, in my opinion, when *Aphytis lingnanensis*, received in California from China in 1948, was mistakenly recorded as originating from *Chrysomphalus aonidum*. I believe *Aphytis lingnanensis* actually came from hidden specimens of *Aonidiella aurantii* mixed in with much larger numbers of *C. aonidum* in the shipments. Probably many *Aphytis holoxanthus* were reared to just a few *Aphytis lingnanensis*, but they were all considered to be the same, hence cultures would have been started with the two species mixed together. Inasmuch as the parasites emerging from the shipments of the Florida red scale *material* were cultured on *Aonidiella aurantii*, a distinct advantage would be given to the *Aphytis* species best adapted to this latter host—in this case, *Aphytis lingnanensis*—and the other *Aphytis* species would be eliminated after a few generations. It has been demonstrated time and again in our laboratory that in mixed-species cultures of *Aphytis*, one species (the one best adapted to the laboratory host or other conditions) will eliminate the other. However, with such events occurring unsuspectedly, it was easy to conclude that *Aphytis lingnanensis* came from *C. aonidum*.

The second source of confusion was that both *Aphytis lingnanensis* and *A. holoxanthus* have pupae pigmented in a similar, if not identical, manner, hence no clue was available in this respect that different species might be involved. Thus, when Flanders in 1954 and DeBach in 1956 saw lingnanensis-type pupae on *C. aonidum* they assumed that the parasite species was *A. lingnanensis*. This emphasizes the fact that while pupal pigmentation may be very helpful (DeBach 1959), it should not be used alone for species determination.

An interesting sequel to the solution of the identity of the Israeli Florida red scale *Aphytis*, and one also illustrating the importance of taxonomy to biological control, lies in the identity of the *Aphytis* attacking *Aonidiella aurantii* in Israel. The shipments (S. & R. Nos. 1934 and 1937) from Israel to California early in 1960 included isolated and parasitized *Aonidiella aurantii* in addition to the *Chrysomphalus aonidum* material already discussed. A culture was started of the *Aphytis* emerging from *Aonidiella aurantii* and designated *Aphytis* "1934." In Israel this species attacking *Aonidiella aurantii* had also been assumed to be *Aphytis lingnanensis*. However, reciprocal crossing tests between *Aphytis* "1934," *Aphytis lingnanensis*, and *Aphytis holoxanthus* yielded no hybrid progeny whatsoever. Also, microscopic study of slide-mounted specimens revealed that consistent and definite differences are evident between *Aphytis* "1934," *Aphytis lingnanensis*, and other described species. *Aphytis* "1934" is described under the name *Aphytis coheni* later in this paper. The recognition of *Aphytis* "1934" as a new species gives entomologists another parasite of *Aonidiella aurantii* for trial in various countries. Otherwise this species might have been overlooked indefinitely, or, as actually happened in Cyprus in 1959 (B. J. Woods, personal communication; DeBach, unpublished data), the parasite of *C. aonidum*, *Aphytis holoxanthus*, might have been imported from Israel for colonization against *Aonidiella aurantii* in the belief that it was *Aphytis lingnanensis* and was identical with the parasite (*Aphytis coheni*) occurring on *Aonidiella aurantii* in Israel and with *Aphytis lingnanensis* elsewhere. Now, arrangements are being made to import *Aphytis coheni*, which definitely is an important parasite of *Aonidiella aurantii* in Israel, into Cyprus, and it is currently being colonized in California.

SYSTEMATICS

The information to be presented in this paper ties in strongly with two previous works. Compere (1955) furnished the basic work on the genus *Aphytis* and his terminology is followed here. In addition to Compere's work, several species which are most likely to be confused with those described as new herein were described or discussed

by DeBach (1959). All descriptions and discussion in the present study are based upon cleared specimens mounted in Hoyer's medium as described by DeBach (1959). All study of specimens was done with a stereoscopic microscope using from 15× to 120× magnification. The following key combines features from Compere (1955) and DeBach (1959). All the species discussed have similar-appearing, predominantly yellow adults in life.

KEY TO SOME MORE EASILY CONFUSED SPECIES AND GROUPS OF *APHYTIS* FEMALES

1. Posterior margin of propodeum without unusually large, overlapping crenulae 2
   Posterior margin of propodeum with unusually large, overlapping crenulae 5
2. Mesoscutum rarely with as many as 12 setae 3
   Mesoscutum always with 12 or more setae 4
3. Antennal club usually less than three times as long as wide, and the thoracic setae comparatively coarse and dusky ..... **mytilaspidis** group
   Antennal club usually three times as long as wide or longer, and the thoracic setae comparatively fine and pale ..... **chrysomphali** group
4. Thoracic sterna dusky ..... **lepidosaphes**
   Thoracic sterna immaculate, or nearly so ..... **immaculatus**
5. Thoracic sterna more or less dusky 6
   Thoracic sterna immaculate 7
6. Front wings basad of the speculum usually with 70 or more setae, setae on sides of abdomen very distinct and coarse (120× magnification), 12–14 coarse, dark setae on mesoscutum ..... **coheni**
   Front wings basad of the speculum usually with 40–50 setae, setae on sides of abdomen indistinct (nearly invisible) at 120× magnification, 10–12 paler setae on mesoscutum ..... **lingnanensis**
7. Setae on mesoscutum dark and coarse (resembling *mytilaspidis* group), antennae noticeably dusky, not especially long and slender, club no more than 3½ times as long as wide, setae on head fairly distinct but pale at 120× magnification ..... **holoxanthus**
   Setae on mesoscutum relatively thin and pale (resembling *chrysomphali* type), antennae pale to slightly dusky, long and slender, club nearly four times as long as wide, setae on head very indistinct, often invisible, at 120× magnification .. **melinus** and **fisheri**

DESCRIPTIONS

Aphytis holoxanthus, new species

Distinguishing Characters.—In addition to the most obvious characters in the preceding key, the pupa has a dark, pigmented pattern on the venter of the thorax and abdomen much like *A. lingnanensis* but perhaps with less pigment toward the tip of the abdomen. This pattern separates *A. holoxanthus* from *A. melinus* (pigment or venter of pupal thorax only) and from *A. fisheri* and *A. lepidosaphes* (no dark pigmentation on pupa) (see DeBach 1959). Body of adult female wholly yellowish, no fuscous areas or furcal pigmentation. Longest forewing fringe hairs about 1.5 times as long as setae on the edge of the marginal vein. Setae on sides of abdomen indistinct at 120× magnification. Ten to twelve coarse dark setae clearly evident on the mesoscutum at 120× magnification; those on the pronotum are indistinct by comparison. Approximately 35–50 setae on the forewing basad of the speculum. Posterior margin of propodeum with 6–7 large overlapping crenulae on each side. A biparental species, with males common. Males like females in color, without dusky markings or lines.

Extensive laboratory mating tests utilizing pure cultures of various species in reciprocal crossing attempts have shown that Aphytis holoxanthus will not cross with *A. lingnanensis*, *A. fisheri*, *A. melinus*, or *A. coheni*.

In Compere's key (1955), *Aphytis holoxanthus* would run to *A. lingnanensis*. It is easily distinguished by the characters given in the author's key and by the previous discussion, the most obvious difference being that *A. lingnanensis* possesses dusky thoracic sterna whereas *A. holoxanthus* is wholly yellow in life and colorless in preserved and cleared slide-mounted specimens.

Aphytis holoxanthus was first received in the insectary of the Department of Biological Control at Riverside, California, on July 16, 1959, from D. W. Jones, of the U. S. Department of Agriculture Parasite Introduction Laboratory at Moorestown, New Jersey. A culture was started in Riverside using *Aspidiotus hederae* and *Aonidiella aurantii* as laboratory hosts. Jones also sent live material to Florida and Texas during 1959 for colonization against *Chrysomphalus aonidum*. Token colonizations of *Aphytis holoxanthus* have been made in California against *Aonidiella aurantii* without much expectation of success. Jones had received material earlier in 1959 through the cooperation of I. Cohen and David Nadel of the Citrus Marketing Board in Israel. They had reared and colonized *Aphytis holoxanthus* in large numbers for control of *C. aonidum*. Their original material was received in February 1956 from S. K. Cheng in Hong Kong and was obtained from the Florida red scale, *C. aonidum*, there. This material was cultured in Dr. E. Rivnay's laboratory in Israel. Cheng made additional substantial shipments to Israel during 1956 and 1957.

In order for us to double check the authenticity of our first culture, additional material, which had been reared on *Chrysomphalus aonidum* in the laboratory, was sent direct from Israel by David Nadel. We received this on January 29, 1960, and the shipment data is recorded under S. & R. No. 1937–5, Memo 60–12. A culture was started on *Aspidiotus hederae* which later was combined with the culture which had been obtained in July 1959 from Jones. The type material was derived from this combined culture reared on *A. hederae*.

Cotypes of *Aphytis holoxanthus* are to be deposited in the U. S. National Museum, in the British Museum, and in the Collection of the Department of Biological Control, University of

California at Riverside. Three slides, each bearing 20 to 30 adults of both sexes under one cover slip and about 10 mature pupae under another cover slip, will be deposited in each institution. The specimens were cleared and mounted in Hoyer's medium as described by DeBach (1959). They represent parasites reared in the insectary at Riverside on *Aspidiotus hederae*, an insectary host.

Aphytis coheni, new species

Distinguishing Characters.—In addition to the most obvious characters given in the preceding key, the pupa has a dark, pigmented pattern on the venter of the thorax and abdomen similar to *A. lingnanensis* and also similar to the *A. holoxanthus* pupa. This pattern separates *A. coheni* from *A. melinus* (pigment only on venter of pupal thorax) and from *A. fisheri* and *A. lepidosaphes* (no dark pigment on pupa) (see DeBach 1959). Body of the adult female generally yellowish, but with a dark line medially on the posterior margin of the scutellum and with distinctly dusky pigmented areas on the thoracic sterna much as in *A. lepidosaphes* and more pronounced than in *A. lingnanensis*. Longest forewing fringe hairs a little longer than the setae on the edge of the marginal vein. Setae on head fairly distinct but pale, at 120× magnification. Wing seta and hair color resembling *A. lepidosaphes*, a little more fuscous than *A. lingnanensis* or *A. holoxanthus*. Ten setae readily visible on the pronotum at 120× magnification—as clear as those on the mesoscutum. Posterior margin of propodeum with at least seven large overlapping crenulae on each side. One to several very faint fuscous bands visible on anterior abdominal sterna at 120× magnification (fully cleared specimens only). Antennae quite dusky when cleared, more so than *A. holoxanthus*. Club about three times as long as wide, somewhat shorter than *A. holoxanthus*. A biparental species, with males common. Males like females, in having dusky thoracic sterna.

Extensive laboratory mating tests utilizing pure cultures of various species in reciprocal crossing attempts have shown that *Aphytis coheni* will not cross with *A. holoxanthus* or with *A. lingnanensis*. In Israel, where our cultures originated, both *A. coheni* and *A. holoxanthus* were thought to be *A. lingnanensis*. As far as is known, *A. lingnanensis* does not occur in Israel. *Aphytis coheni* and *A. holoxanthus* may occur on the same individual citrus tree in Israel, but *A. coheni* parasitizes the California red scale, *Aonidiella aurantii*, whereas *Aphytis holoxanthus* parasitizes the Florida red scale, *Chrysomphalus aonidum*.

Aphytis coheni was first received in the insectary of the Department of Biological Control at Riverside, California, on January 19, 1960, in a shipment under S. & R. No. 1934, Memo 60–3, and on January 28, 1960, under S. & R. No. 1937–5, Memo 60–11. These shipments contained parasitized *Aonidiella aurantii* collected from citrus trees at Ashkelon, Israel, by David Nadel. In Riverside successful culture resulted from using either *Aonidiella aurantii* or *Aspidiotus hederae* as hosts. The type material resulted from this culture using *Aspidiotus hederae* as a host. *Aphytis coheni* is known to the author only from Israel, where, according to past correspondence with I. Cohen and others, it (or at least *Aphytis*) often maintains satisfactory biological control of *Aonidiella aurantii* on old citrus trees. Whether *Aphytis coheni* is native or is an accidental introduction into Israel is unknown. The latter possibility seems the most likely inasmuch as, to the author's personal knowledge, *Aphytis coheni* was not found in nearby Greece on *Aonidiella aurantii* in 1957 where it presumably should have occurred if *Aphytis coheni* were native, hence had been present for a lengthy period, in Israel. *Aphytis coheni* was colonized against *Aonidiella aurantii* in the field in southern California beginning in July, 1960. It is an addition to the known species of *Aphytis* which, in various parts of the world, attack *Aonidiella aurantii* as a preferred or at least highly acceptable host in the field.

Aphytis coheni is named after Mr. I. Cohen, of the Citrus Marketing Board of Israel, who has been instrumental in bringing about two outstandingly successful examples of complete biological control in Israel—that of the mealybug, *Pseudococcus citriculus* Green (= *comstocki* in litt.), by *Clausenia purpurea* Ishii in the 1940's, and that of the Florida red scale, *Chrysomphalus aonidum*, by *Aphytis holoxanthus* in the late 1950's.

Cotypes of *Aphytis coheni* are to be deposited in the U. S. National Museum, in the British Museum, and in the collection of the Department of Biological Control, University of California at Riverside. Three slides, each bearing 20–30 adults of both sexes under one cover slip and about 10 mature pupae under another cover slip, will be deposited in each institution. The specimens were cleared and mounted in Hoyer's medium as described by DeBach (1959). They represent parasites reared in the insectary at Riverside on *Aspidiotus hederae*, an insectary host, on lemon fruit.

REFERENCES CITED

Compere, Harold. 1955. A systematic study of the genus *Aphytis* Howard (Hymenoptera, Aphelinidae) with descriptions of new species. Univ. California Publ. Ent. 10(4): 271–320.

DeBach, Paul. 1959. New species and strains of *Aphytis* (Hymenoptera, Eulophidae) parasitic on the California red scale, *Aonidiella aurantii* (Mask.), in the Orient. Ann. Ent. Soc. America 52(4): 354–62.

DeBach, Paul, and **Pelagija Sisojević** 1960. Some effects of temperature and competition on the distribution and relative abundance of *Aphytis lingnanensis* and *A. chrysomphali* (Hymenoptera: Aphelinidae). Ecology 41(1): 153–60.

Flanders, Stanley E. 1953. Hymenopterous parasites of three species of oriental scale insects. Bol. Lab. Zool. Gen. Agr. (Filippo Silvestri) Portici 33: 10–28.

OBSERVATIONS ON AEDES MELANIMON AND A. DORSALIS IN NEVADA[1]

H. C. CHAPMAN

Entomology Research Division, Agric. Res. Serv., U.S.D.A.[2, 3]

ABSTRACT

In biological studies on *Aedes melanimon* Dyar and *A. dorsalis* (Meigen), *A. melanimon* was found capable of breeding in moderately alkaline areas but was most abundant in fresher water. *Aedes dorsalis*, while very abundant in fresh water, was usually the sole occupant in highly alkaline areas. Larvae of these two species were often associated with *A. nigromaculis* (Ludlow). *A. melanimon* was seldom an important daytime-biting pest. The principal daytime-biting species were *dorsalis* and *nigromaculis* and these species were absent whenever daytime-biting populations of *melanimon* were observed.

Until 1955 *Aedes melanimon*, described from California by Dyar (1924), was considered to be a synonym of *Aedes dorsalis*. Barr (1955) resurrected *melanimon* as a valid species on the basis of differences in the adult male genitalia. Both Bohart (1956) and Richards (1956) presented reliable characters for the separation of adult females and larvae of these two species. Richards (1956) and Richards et al. (1956) reported *melanimon* from California, Colorado, Montana, Nebraska, Nevada, Washington, New Mexico, Idaho, and Utah, and relatively abundant in the first five States. Richards collected *melanimon* and *dorsalis* adults in about equal numbers from many Nevada counties. Bohart also listed *melanimon* from Oregon. *A. dorsalis* has a Holarctic distribution, and was reported from 30 states and Canada by Carpenter and LaCasse (1955).

Previous published records of *dorsalis* concerning its distribution, vector potentiality, pestiferousness, preferred larval habitats, and salinity tolerances in States within the range of *melanimon* have had to be re-examined. Little is known of the relationship of *melanimon* to many of these factors; this study was undertaken to provide some of this information since both *dorsalis* and *melanimon* occur abundantly in Nevada.

Laboratory Observations

From July through September 1959, 200 larval collections were made in and around irrigated areas in many counties but principally Churchill, Lyon, and Washoe. Usually a minimum of 50 larvae of *dorsalis* and/or *melanimon* were identified in the laboratory from each sample and the composition of each species was ascertained. The following information was obtained about the water in which the larvae were breeding: hydrogen-ion concentration (pH) by the Beckman pH meter, total concentration of soluble salts by a Solu Bridge soil tester, and total chlorides by the silver nitrate titration method. Notes were also taken on larval habitat, the rapidity of larval development, adult biting habits in the field, and oviposition in the laboratory. The presence and relative abundance in the samples of *Aedes nigromaculis* (Ludlow) and *A. vexans* (Meigen) were also noted.

Table 1 shows an excellent correlation between the various population levels of *melanimon* and *dorsalis* and the pH, total soluble salts, and chlorides, especially the last two. *A. melanimon* appears to prefer a lower pH and lesser amounts of total soluble salts and chlorides than *dorsalis*. However, one sample which had 12,160 p.p.m. of total soluble salts and 2,824 p.p.m. of chlorides contained only *melanimon* larvae, and larvae of this species were found sparsely in waters containing a maximum of 39,424 p.p.m. of total soluble salts and 17,750 p.p.m. of chlorides. This is a considerable extension of the known salt tolerance of *melanimon*, since Bohart reported it in water containing salts up to 18,000 p.p.m. (1.8%). *A. dorsalis*, although often found in fresh water, is much more tolerant and prefers or tolerates higher amounts of total soluble salts, chlorides, and pH. Rees and Nielsen (1947) reported *dorsalis* completing its aquatic development in Utah in a slightly higher salt concentration of 120,000 p.p.m. (12%) and with the pH ranging from 7.0 to 9.3 with a mean of 8.3. Telford (1958) in California reported *dorsalis* breeding in waters containing dissolved salts ranging from 1,000 to 80,500 p.p.m. (0.1% to 8.05%).

According to data presented in table 2, the largest number of samples (106) were taken in irrigated fields with slightly higher breeding of *dorsalis*, whereas *melanimon* was more prevalent in samples collected from roadside ditches and potholes, sloughs, and drain ditches. Seep areas, which are usually highly alkaline, produced mostly *dorsalis*.

In data not shown, *Aedes nigromaculis* was noted in 83 of these samples, the waters of which had the following ranges: pH 4.7 to 9.2; total soluble salts 122 to 2,624 p.p.m.; and chlorides 18 to 391 p.p.m. Most of these collections were made in irrigated fields, with a preponderance of

[1]Accepted for publication, March 11, 1960.

[2]In cooperation with the Nevada Agricultural Experiment Station.

[3]David F. Grill assisted in these studies.

the remainder in roadside ditches and potholes. Only 5% of the samples contained larvae of *vexans*, the only other *Aedes* species found in the samples, and these indicated ranges of 6.5 to 8.0 for the pH, 230 to 1,216 p.p.m. for total soluble salts, and 27 to 692 p.p.m. for chlorides. *A. vexans* larvae occurred mostly in roadside ditches and potholes and drain ditches. Larvae were noted only twice in irrigated fields in 2 years' collecting.

Field Observations

Bohart (1956) mentioned the apparent competition between *nigromaculis*, *melanimon*, and *dorsalis* in irrigated areas in the Great Valley in California, and considered *dorsalis* to be the least successful. Telford (1958) observed that *nigromaculis* and *melanimon* bred in the same general habitat in California, but occupied entirely different niches; he indicated no interaction of *dorsalis* with these species in irrigated pastures. In Nevada it appears that there is considerable interaction between *nigromaculis*, *melanimon*, and *dorsalis*, with the first species the least prevalent in and adjacent to irrigated fields. *A. nigromaculis* was absent in 117 of the 200 samples, the most abundant species in 22, and the sole species in only one. It was noted with *melanimon* in all but 3 of the 83 times it was collected, which indicates both an intimate species and habitat relationship between these species.

Richards (1956) stated that both *dorsalis* and *melanimon* attack man readily, are painful biters, and are important because of their abundance. Two years' observations in many areas of Nevada indicate that the daytime biting activity and importance of *melanimon* is overrated, especially in those areas which also produce sizable numbers of *dorsalis* and *nigromaculis*. Large numbers of daytime-biting *melanimon* were observed only on a few occasions, and these were usually in isolated areas which produced almost solely *melanimon* larvae. Even then *melanimon* females were more timid and flighty. Many times tremendous broods of almost pure *melanimon* were observed, but when these areas were revisited several days following adult emergence, the daytime-biting adults were usually principally *dorsalis* and *nigromaculis* with a few *melanimon*.

Adult females of *melanimon*, *dorsalis*, and *nigromaculis* were allowed to feed to repletion on human hosts in the field and were then collected in vials 20 mm. in diameter and 93 mm. in length and held for oviposition in the laboratory, as reported by Barr and Al-Azawi (1958). Since there were no facilities for controlling the temperature and humidity, the information obtained is not indicative of the complete oviposition potential of these species. However, it does indicate their relative tolerance to adverse conditions (low humidity and high temperature) and shows *melanimon* to be much less tolerant than the other

Table 1.—Summary of pH, total soluble salts, and chlorides, showing data obtained in *Aedes melanimon* and *dorsalis* larval collections made during July-September, 1959.

Number of samples	Percent of		pH		Soluble salts (p.p.m.)		Chlorides (p.p.m.)	
	melanimon	*dorsalis*	Range	Mean	Range	Mean	Range	Mean
22	100	0	4.7–9.4	7.2	141–12,160	891	14–2,824	175
33	76–99	1–25	6.3–8.3	7.2	122–2,880	531	16–692	68
36	51–75	26–50	6.0–8.3	7.0	122–3,968	601	18–1,491	112
34	26–50	51–75	5.7–9.3	7.5	77–6,976	1,060	18–1,882	203
49	1–25	76–99	6.3–9.2	7.7	122–39,424	3,191	14–17,750	771
26	0	100	6.9–10.1	8.1	243–106,176	14,673	18–42,778	3,918

Table 2.—Summary of ecological habitats in which larvae of *Aedes melanimon* and *dorsalis* were collected July-September, 1959.

Percent of larvae as		Irrigated fields	Roadside ditches and potholes	Sloughs	Seep areas	Drain ditches	Miscellaneous
melanimon	*dorsalis*						
100	0	7	11	2	0	2	0
76–99	1–25	16	11	4	0	1	1
51–75	26–50	19	8	3	1	4	1
26–50	51–75	24	4	2	3	1	0
1–25	76–99	27	3	4	11	3	1
0	100	13	2	0	9	0	2

two species. Only 10 *melanimon* females out of several hundred specimens remained alive for the 5 days required for ovipositing in the vials, and these eggs ranged in number from 11 to 84 with a mean of 33 per female. Less mortality was noted in both *dorsalis*, which laid a mean number of eggs of 67 ranging from 1 to 191, and *nigromaculis*, whose mean and range of eggs deposited was 61 and 1 to 178, respectively.

Thousands of *dorsalis* and *melanimon* adults and larvae were collected and examined during this study and the previous year, and the writer agrees with Richards that the mesonotal markings of *dorsalis* vary considerably but those of *melanimon* exhibit almost no variation. The taxonomic characters mentioned by both Richards and Bohart for the separation of adult females (color scaling of anal vein) and larvae (size of mesonotal hair 1) appear to be reliable for Nevada material.

A. dorsalis larvae were first noted in 1959 on February 26 and those of *melanimon* on April 16. Breeding of *dorsalis* was last observed on November 5 in 1958 and on November 10 in 1959 whereas *melanimon* was noted as late as November 21 and 3 in the respective years. The time required for the aquatic cycle of the two species appears to be identical and is dependent on temperature. Development required 21 to 24 days in April but only 6 to 8 days during the warmest summer months. *A. nigromaculis* completed its aquatic cycle in a minimum of 5 days, and when in the company of *dorsalis* and *melanimon* was often the first species to hatch, comprised the largest specimens present, and the first species to pupate and emerge as adults. Thirteen successive broods of *dorsalis* and *melanimon* were produced in one field during a season. The number of broods was dependent only on the number of irrigations to which the area was subjected during the year.

REFERENCES CITED

Barr, A. R. 1955. The resurrection of *Aedes melanimon* Dyar. Mosquito News 15(3): 170–2.

Barr, A. R., and **A. Al-Azawi.** 1958. Notes on oviposition and the hatching of *Aedes* and *Psorophora* mosquitoes (Diptera-Culicidae). Univ. Kansas Sci. Bull. 39(6): 263–73.

Bohart, R. M. 1956. Identification and distribution of *Aedes melanimon* and *Aedes dorsalis* in California. Proc. and Papers 24th Ann. Confer. California Mosquito Control Assoc., pp. 81–83.

Carpenter, S. J., and **W. J. LaCasse.** 1955. Mosquitoes of North America. Berkeley: Univ of California Press. 360 pp.

Dyar, H. G. 1924. Two new mosquitoes from California. Insec. Inscit. Menstr. 12: 125–7.

Rees, D. M., and **L. T. Nielsen.** 1947. On the biology and control of *Aedes dorsalis* (Meigen) in Utah. Proc. New Jersey Mosquito Exterm. Assoc. 34: 160–5.

Richards, C. S. 1956. *Aedes melanimon* Dyar and related species. Canadian Ent. 88(6): 261–9.

Richards, C. S., L. T. Nielsen, and **D. M. Rees.** 1956. Mosquito records from the Great Basin and the drainage of the lower Colorado River. Mosquito News 16(1): 10–17.

Telford, A. D. 1958. The pasture *Aedes* of central and northern California. Seasonal history. Ann. Ent. Soc. America 51(4): 360–5.

SOME ABNORMALITIES IN THE FOXGLOVE APHID IN NORTHEASTERN MAINE[1]

H. E. WAVE,[2,3] W. A. SHANDS,[2] AND G. W. SIMPSON[4]

ABSTRACT

Unprecedented numbers of alate foxglove aphids, *Myzus solani* (Kltb.), developed at Presque Isle, Maine, in the late summer and fall of 1956 and 1957 on potato plants not treated with insecticides. Many of the alatae exhibited abnormalities in both the number and and position of the wings. Also atypical venation in the forewings was common in both abnormal and normal alates. Abnormally alate forms were observed in the spring migrant forms maturing on *Hieracium* spp., hawkweed, an overwintering host. These phenomena may be genetic manifestations due to the crossing of two strains of the aphid or the effects from unusual environmental conditions, including subnormal temperatures.

The foxglove aphid, *Myzus solani* (Kltb.), an important pest of potatoes in northeastern Maine, was reported by Patch (1928) as having common foxglove, *Digitalis purpurea* L., as its primary host. Our studies (Wave et al. 1956) showed that, although foxglove is an overwintering or primary host, and hemp nettle, *Galeopsis Tetrahit* L., may be another, the far most common and important primary host in northeastern Maine is hawkweed, *Hieracium* spp. They also showed that the aphid inhabits hawkweed throughout the summer and that apterous males develop on it in the fall.

Patch also said that in late summer the aphid moves from various secondary hosts to *D. purpurea*, where apterous males later develop. Our observations suggest that fall migrants may

[1]Accepted for publication March 21, 1960.

[2]Entomology Research Division, Agricultural Research Service, U. S. D. A.

[3]Resigned August 1958.

[4]Maine Agricultural Experiment Station.

occur in Maine because some of the alatae maturing late in the summer find their way to and deposit nymphs on hawkweed. We have not determined whether these nymphs become the oviparae. Reinfestations or supplemental infestation of hawkweed through return flights is probably of minor importance, for our observations indicate that only very small numbers of the alatae settle and deposit nymphs on this plant.

During the period 1941–55 only a few alate foxglove aphids were found maturing on potato plants at any time during the season, with only trace numbers late in the summer. However, appreciable numbers of alatae developed on potatoes at Presque Isle in 1956 and 1957, particularly in late summer and fall on plants to which no insecticide had been applied. Among these alatae the abnormalities included complete absence of some wings and incomplete development of others. Furthermore, atypical venation of the forewings also occurred in many. This paper contains data on the nature and prevalence of the abnormalities in both years, and suggests possible reasons for their occurrence.

PREVALENCE OF WINGED FORMS

Late in August 1956 there was a sharp increase in the number of nymphs destined to be alate. Nymphs with abnormal wing pads were first observed on August 30. During the next few days the abundance of both normal and abnormal alatiform nymphs increased. To determine their prevalence, counts were made on untreated potatoes in small plots on September 6 and 7. In each plot all leaves of enough consecutively occurring plants were examined to find a total of 25 nymphs nearing maturity. Records were made to show the number destined to be apterous adults, normal alates, and abnormal alates. This procedure appeared to be an approach to sampling the progeny of a single spring migrant for each plot, since oat barriers separated the plots from each other (Shands et al. 1950). The counts showed that alate aphids were developing in at least 54 of the 57 plots examined. Of the 1,425 large nymphs observed, 17 percent were destined to be alate adults, and among these, 34 percent were abnormal. We have no comparable data for 1957, but abnormal specimens were relatively much less abundant than in 1956.

NATURE AND PREVALENCE OF THE WING ABNORMALITIES

The results of examinations of abnormally alate specimens taken at random from the plots of untreated potato plants are shown in table 1.

In 1956 most of these specimens were collected as large nymphs and reared to maturity, and in 1957 they were collected as adults. Of the specimens examined in 1956, 6 percent had only three wings, 80 percent had two, 7 percent had one, and 7 percent had only wing rudiments. Among the specimens having only two fully developed wings, with or without wing rudiments, 50 percent had them on the right side, 44 percent on the left, and 6 percent had one on each side. Among specimens with only two fully developed wings on one side, 51 percent had them on the right side and 49 percent on the left.

In 1957, 5 percent of the specimens had only three wings, 76 percent had two, 3 percent had

Table 1.—Wing abnormalities in alate foxglove aphids taken from potato plants as adults or as nymphs and reared to maturity in the falls of 1956 and 1957.

Number and position of wings	Number of specimens	
	1956	1957
Three fully developed wings		
Missing wing		
Right mesothoracic	2	0
Right metathoracic	1	0
Fourth wing rudimentary		
Right mesothoracic	1	2
Right metathoracic	1	0
Left mesothoracic	0	3
Two fully developed wings		
Missing wings		
Right	17	14
Left	18	22
Rudimentary wings		
Both on right	3	3
Both on left	7	11
Right mesothoracic	1	2
Left mesothoracic	4	0
Right metathoracic	8	10
Left metathoracic	4	8
Both mesothoracic	2	0
Both metathoracic	2	0
One fully developed wing		
Mesothoracic		
Right	1	0
Left	2	0
Right, all others rudimentary	2	0
Right, plus rudimentary right metathoracic	0	1
Left, plus rudimentary left metathoracic	0	1
Metathoracic		
Left, all others rudimentary	1	0
Right plus right rudimentary mesothoracic	0	1
Rudimentary wings only		
All four	2	3
Three		
Both left plus right metathoracic	1	0
Both right plus left metathoracic	0	1
Two		
Both right	1	1
Both left	2	2
Metathoracic	0	1
Left meso- and right metathoracic	0	1
One		
Right mesothoracic	0	1
Left mesothoracic	0	2
Right metathoracic	0	1
Left metathoracic	0	1

one, and 15 percent had only wing rudiments. Fifty-nine percent of those with only two fully developed wings, with or without wing rudiments, had them on the right side and 41 percent on the left. Of those with only two fully developed wings on one side of the body 39 percent had them on the left side and 61 percent on the right.

Examination of all alatae maturing in outdoor cages on three species of host plants in 1955 and on hawkweed in 1956 and 1957 (table 2) revealed that abnormally alate specimens developed in the last 2 years, and that they occurred only on hawkweed. All the abnormal specimens in 1956 matured between July 10 and 25, and the lone specimen in 1957 matured on June 24. Of those maturing in 1956, 8.3 percent were abnormal, as compared with 1.1 percent of those maturing in 1957. Out of the total of 15 abnormal specimens maturing in the outdoor cages in 1956 and 1957, 2 had only three fully developed wings, 11 had two, and 2 had only wing rudiments. Three of the two-winged specimens had both wings on the right side and eight had them on the left.

Table 2.—Alate foxglove aphids reared on three species of host plants in outdoor cages and the percent abnormally alate, 1955–57.

Year	Average number per square foot	Percent abnormally alate
	Hawkweed	
1955	35	0
1956	15	8.3
1957	7	1.1
	Hemp nettle	
1955	34	0
	Foxglove	
1955	44	0

Atypical venation occurred in the forewings of both abnormal and normal alates maturing on caged plants and on mint, *Mentha arvensis* L. growing in the greenhouse in the fall of 1956. The irregularities in venation included loss of whole veins, incomplete or interrupted veins, and irregular branching. Apparently atypical venation in this species of aphid is not uncommon.

DISCUSSION

No clear-cut reason can be suggested for the unprecedented abundance of the alatae of the foxglove aphid on potatoes in late summer and early fall, or for the large number of alate individuals showing abnormalities taken from potatoes and hawkweed. The phenomenon may be genetic in nature or due to unusual environmental conditions. If genetic, any crossing must have occurred earlier by at least one sexual generation.

Two strains of the foxglove aphid have been reported, one with apterous and the other with alate males. Hille Ris Lambers (1949) stated that apterous males occurred in the Netherlands on a number of different plants. In Germany, Heinze and Profft (1940) reported alate males. At Presque Isle an alate male developed on caged hawkweed in the fall of 1956, indicating that two strains of the aphid may occur in Maine. In that event crossing of the two strains could have resulted in the abnormalities observed in 1956 and 1957.

Environmental factors may have caused the abnormalities. Shands and Simpson (1948) and Lal (1952, 1955) have reviewed some of the results of studies showing the effect of various factors upon the development of alatae. Several workers, including Ackerman (1926) and Bonnemaison (1951), have considered that crowding was the cause, either directly or indirectly. However, MacGillivray and Anderson (1958) found this was not always so for the potato aphid. Our observations show that, except for potatoes, aphid populations are generally low on all hosts of the foxglove aphid in northeastern Maine. Crowding seldom if ever occurs, even on potatoes; it definitely appeared not to be a factor in the plots of potatoes where our observations were made.

Table 3.—Mean monthly temperatures for July and August at Presque Isle and departures from the normal[a], 1942–1957.

Year	July (°F)		August (°F)	
	Temperature	Departure from normal	Temperature	Departure from normal
1942	64.3	−1.7	64.7	+0.8
1943	66.8	+0.8	63.2	−0.7
1944	67.4	+1.4	68.7	+4.8
1945	67.3	+1.3	65.9	+2.0
1946	64.8	−1.2	63.7	−0.2
1947	70.5	+4.5	66.9	+3.0
1948	67.1	+1.1	66.3	+2.4
1949	68.6	+2.6	66.1	+2.2
1950	65.4	−0.6	63.2	−0.7
1951	65.7	−0.3	63.1	−0.8
1952	71.2	+5.2	66.2	+2.3
1953	65.9	−0.1	62.7	−1.2
1954	63.0	−3.0	61.5	−2.4
1955	67.6	+1.6	65.8	+1.9
1956	62.2	−3.8	60.3	−3.6
1957	63.5	−2.5	60.3	−3.6

[a]Based on records covering 33 years.

Several investigators have reported on the effects of environmental factors, especially temperature and light, upon the genetic mechanism of wing development in some aphids. Ewing (1916) found that there was an optimum temperature for the production of apterous forms and two optima for the production of alatae in

the apple grain aphid, *Rhopalosiphum fitchii* (Sand.). Working with the same aphid, Wadley (1923) confirmed these results and he showed that of several temperature levels, fewer winged forms developed at 65° F. than at either higher or lower temperatures. Gregory (1917), working with the pea aphid, *Macrosiphum pisi* (Harris), interpreted Ewing's results not as a direct effect of temperature on wing development, but as an indirect effect due to the altered nutrient condition of the host plant as food for the aphid. Davidson (1924), testing light periodicity as a factor in wing development, also concluded that the activation of the aphids' wing-producing mechanism was an indirect effect—that of starvation—brought about as a result of altered food value of the imbibed plant juices due to reduced photosynthesis. Shull (1942) concluded that wing production in the potato aphid, *Macrosiphum solanifolii* (Ashm.), was influenced through the same mechanism by both light and temperature. He further stated that either of these factors may begin the process of wing production, and both factors operating simultaneously hasten the change from the apterous state.

The appearance of appreciable numbers of alate foxglove aphids and of abnormal alates may have been caused by unusually low temperatures. Table 3 shows that the mean temperatures for July and August at Presque Isle were 2.5° F. and 3.6° below average in 1957 and 3.8° and 3.6° below average in 1956, respectively. Although such subnormal temperatures were nearly reached in 1954, during a 16-year period they occurred only in 1956 and 1957. Further, if the important factor is the effect of subnormal temperature upon the mother aphid, it must have been most pronounced during the latter part of August. The mean daily temperature during the last 12 days of August was 8.1° below the August mean for 1956 and 5.2° below for 1957. Below-normal temperature during the critical period before deposition of the nymphs could also have influenced the production of the abnormal alates maturing on caged hawkweed in June and July.

The mechanism producing the abnormally winged foxglove aphids may have been tied up with the insect's hormone system. Johnson (1958) reporting on some intermediates of *Aphis craccivora*, produced by parasitization, concluded that the parasite caused interference with the hormone system of the alatiform nymph. Wigglesworth (1954) has stated that low temperature upsets the hormone balance very slightly in favor of the juvenile hormone. Furthermore, he stated that juvenile hormones can have a purely local effect, which strongly suggests that the hormone is not merely catalysing some cellular reaction but actually taking part in the metabolism of the cell itself. Perhaps low temperature was the condition which upset the hormone balance in the foxglove aphid, altering especially the roles played by timing and concentration of the juvenile hormone prior to the final molt. This could have resulted in the suppression of normal adult wing characters.

Similarly, low temperature may have caused the mother aphid to deposit nymphs of which a larger than usual percentage were destined to be alatoid.

REFERENCES CITED

Ackerman, L. 1926. The physiological basis of wing production in the grain aphid. Jour. Exptl. Zool. 44: 1–61.

Bonnemaison, L. 1951. Contribution à l'étude des facteurs provoquant l'apparition des formes ailées et sexuelles chez les Aphidinae. Ann. Inst. Natl. Recherche Agron. (C) 2(1–2): 1–380.

Davidson, J. 1924. Factors which influence the appearance of the sexes in plant lice. Science 59: 364.

Ewing, H. E. 1916. Eighty-seven generations in a parthenogenetic pure line of *Aphis avenae* Fabricius. Biol. Bull. 31: 53–112.

Gregory, L. H. 1917. The effect of starvation on wing development of *Macrosiphum destructor*. Biol. Bull. 33: 296–303.

Heinze, K., and **J. Profft.** 1940. Ueber die an der kartoffellebenden Blattläusarten und ihren Massenwechsel im Zusammanhang mit dem Auftreten von Kartoffelvirosen. Mitteil. Biol. Reichsanst. 60: 1–164.

Hille Ris Lambers, D. 1949. Contributions to a monograph of Aphididae of Europe. Temminckia 8: 182–323.

Johnson, B. 1958. Influence of parasitization on form determination in aphids. Nature [London] 181(4603): 205–6.

Lal, R. 1952. Effect of mal-nutrition due to crowding and starvation of alate-parents on the production of alate-offspring among aphids. Indian Jour. Ent. 14: 11–19.

1955. Effect of the water content of aphids and their host plants on the appearance of alatae. Indian Jour. Ent. 17: 52–62.

MacGillivray, M. E., and **G. B. Anderson.** 1958. Production of apterous and alate progeny by apterous and alate viviparae of *Macrosiphum solanifolii* (Ashm.) (Homoptera: Aphididae). Canadian Ent. 90: 241–5.

Patch, Edith M. 1928. The foxglove aphid on potato and other plants. Maine Agric. Expt. Sta. Bull. 346: 49–60.

Shands, W. A., and **G. W. Simpson.** 1948. The production of alate forms of *Myzus persicae* on *Brassica campestris* in the greenhouse. Jour. Agric. Res. 76(7–8): 165–73.

Shands, W. A., G. W. Simpson, P. M. Lombard, R. M. Cobb, and **P. H. Lung.** 1950. Control of aphids on potatoes with DDT when used with fungicides. Maine Agric. Expt. Sta. Bull. 480: 1–41.

Shull, A. F. 1942. The mechanism through which light and heat influence genetic factors for wing development in aphids. Jour. Exptl. Zool. 89(2): 193–95.

Wadley, F. M. 1923. Factors affecting the proportion of alate and apterous forms of aphids. Ann. Ent. Soc. America 16: 279–303.

Wave, H. E., W. A. Shands, and **G. W. Simpson.** 1956. Recently discovered primary hosts of the foxglove aphid. Jour. Econ. Ent. 49(1): 137.

Wigglesworth, V. B. 1954. The Physiology of Insect Metamorphosis. Cambridge University Press. 152 pp.

MORPHOLOGY OF THE PLEUROSTERNAL REGION OF THE PTEROTHORAX IN INSECTS[1]

RYUICHI MATSUDA

Department of Entomology, University of Kansas, Lawrence

ABSTRACT

In the pterothorax of primitive insects the sternum was exposed. The precoxal suture was complete throughout the entire pleural wall, including the episternum and epimeron, and divided it into the outer anapleural and inner katapleural rings. The anapleural region was composed of the anepisternum, preepisternum, ventropleurite, and anepimeron; the katapleural area was composed of the katepisternum, trochantin, and katepimeron. From this probable primitive condition of the pleural wall the pleurosternal region of insects has undergone various modes of modification by fusion and loss of plates, accompanied by increasing sclerotization.

The subcoxal origin of the thoracic pleuron of insects was maintained by Heymons (1899) and by Roonwal (1937, 1939) on the basis of their embryological discoveries in Hemiptera and Orthoptera, respectively. The modern interpretation of the pleurosternal region of the insect thorax is based on this theory.[2] Among recent contributions to this field, the study by Asahina (1954) on *Epiophlebia superstes* Selys (Odonata) and that of Matsuda (1956b) on *Siphlonurus columbianus* McDunnough (Ephemeroptera) have elucidated the morphological features of these two divergent orders of insects. Very significantly, Carpentier (1956) succeeded in homologizing the pleurosternal region, sclerite by sclerite, between *Blatta orientalis* L. (Blattaria) and *Ctenolepisma ciliata* (Thysanura). The comparative study by Matsuda (1956a) on a primitive holometabolous insect, *Agulla adnixa* (Neuroptera), and a primitive hemimetabolous insect, *Blattella germanica* (Blattaria), also showed that the homologies of all pleural sclerites are possible between the two species.

All these recent studies treating morphologically highly important species suggest that it would be possible to homologize the pleurosternal region of the pterothorax throughout the orders of insects if certain principles were followed. To establish homologies of parts of the pleurosternal region of various orders, this paper attempts first to reconstruct a probable primitive structural plan of the pleurosternal region by comparing a series of forms, and by referring to pertinent literature. With this done, homologizing the parts in different orders can relatively easily be attempted in terms of loss and fusion of parts accompanied by sclerotization—which has evidently been the main evolutionary trend of the pterothorax. In many species, of practically all orders, the evolution of the pleurosternal region has reached the point where ancestral structural features are hardly discernable. Therefore, the relatively primitive forms are the ones used as basic materials of study in this paper.

The problems posed above appear to require tremendous efforts, and luck in choosing the right insects for study. However, it was found that this task could be greatly eased by re-examining the previously published drawings of the pleurosternal regions of various groups of insects, and frequent references are made to them in the following pages. Whenever drawings were found to be interesting, they were compared with actual specimens for confirmation.

TERMINOLOGY

Before the morphological evidence for homologies is presented, it is highly desirable to define the terms used in this work. I have attempted to use, for each structure of the pleurosternal region, a name which is neither misleading as to homology nor meaningless, and have been compelled to propose some new names for certain of the structures which lacked English names or whose names in previous use had misleading connotations.

Anapleural cleft.—The membranous cleft separating the anepisternum from the preepisternum. This term, originally used by Ferris, was later changed to *pleural cleft*. Upon being sclerotized this membranous cleft becomes a suture, but the term *pleural suture* is not available for it (see below). Therefore Ferris' earlier name is used.

Anepimeron.—The dorsal part of the epimeron, defined ventrally by the precoxal suture.

Anepisternum.—The dorsal part of the episternum, defined ventrally by the anapleural membrane or suture. This area has been called *anterior basalare* by some workers.

Basalare.—A small sclerite above the anepisternum, located above the basalar cleft when it is present. This plate has been called the *second* or *posterior basalare* by some workers.

Basalar cleft.—This is the *incisura basalare* of La Greca (1949); usually a more or less longi-

[1]Contribution No. 1068 from the Department of Entomology, University of Kansas. This work was aided by a grant from the National Science Foundation. Accepted for publication December 12, 1959.

[2]Snodgrass (1958) has disputed the theory of the subcoxal origin of the pleuron in insects, but that theory is retained here since the origin of the pleuron—whether subcoxal or not—is not the primary concern in this work.

tudinal, membranous cleft in the anepisternum. The term *basalar suture* is used when the cleft is represented by a suture.

Basisternum.—The anterior area of the primary sternum, anterior to the base of the sternal apophysis.

Epimeron.—The area of the pleuron posterior to the pleural suture.

Episternum.—The area of the pleuron anterior to the pleural suture.

Furcasternum.—The posterior area of the primary sternum bearing the sternal apophyses.

Katepimeron.—The ventral area of the epimeron, bounded dorsally by the precoxal suture.

Katepisternum.—The ventral area of the episternum, bounded dorsally by the precoxal suture.

Pleural suture.—The suture dividing the pleuron vertically into the episternum and the epimeron; it extends from the base of the coxa to the wing base, and is represented internally by the pleural ridge.

Pleural ridge.—The endopleural ridge formed by the inflection of the pleural suture.

Precoxal suture.—This is the *pleural costa* of Ferris. Though the area beneath the suture is sometimes strongly inflected to form a costa, it is often rather weakly marked and its internal inflection is also weak. Moreover, Ferris did not name the suture formed externally by this costa, so that *precoxal suture* is substituted for it here. Michener (1944) used this name for the episternal portion of the suture, which, however, extends primitively to the epimeral region.

Poststernum.—The secondary formation behind the furcasternum.

Preepisternum.—The ventral area of the anapleural ring of the subcoxa, defined dorsally by the anapleural cleft or suture. This is the *precoxal bridge*, or the *lateropleurite*, or the *laterosternite*, of some workers.

Presternum.—The area anterior to the basisternum, often set off by the submarginal suture of the basisternum.

Spina.—The median apodemal process located at the ventral intersegmental region.

Subcoxa.—The primitive basal segment of the leg, constituting the definitive pleuron of the thorax.

Sternal apophysis.—The paired endoskeletal structure located on the furcasternum. Also called simply the *furca*.

Trochantin.—A katepisternal sclerite, articulated at its ventral end to the anterior margin of the coxa; often divided into anterior and posterior trochantins, of which the former is articulated with the coxal margin.

Ventropleurite.—A small sclerite located laterad of the furcasternum or the base of the sternal apophysis; often fused with the preepisternum or the sternum, or entirely lost. This is the *laterosternite* of Weber (1928) and Snodgrass (1935). Since its pleural origin is unanimously recognized by principal workers (including Snodgrass and Weber), that name is misleading and *ventropleurite* is proposed to replace it. Crampton (1914) evidently regarded this plate as a part of the sternum, for he said: "These lateral extensions [of the sternum] may become detached to form separate plates, laterosternites, as in the earwig. . . ." The plate he called the laterosternite is, in fact, composed of two plates separated by an oblique suture, the anterior part being actually the preepisternum, and the posterior part alone can be regarded as the ventropleurite (laterosternite), as will be demonstrated later. Many modern workers apparently are still following Crampton, thus confusing the terminology and the homologies of the preepisternum and ventropleurite. The ventropleurite as here accepted is a small sclerite located lateral to the furcasternum or to the base of the sternal apophysis. It is often fused with the preepisternum or with the sternum, or completely lost.

THE THEORIES OF WEBER AND FERRIS, WITH SPECIAL REFERENCE TO THE MORPHOLOGY OF THE STERNUM

These theories regarding the pleurosternal region of the insect thorax are similar in certain respects but are definitely different in others. Occasionally they have been confused in the past, and the credit due has not been given to the proper author.

Weber (1928) was the first author, so far as I am aware, who put forward the concept of "the cryptosternite," which is the invaginated sternum seen in the holometabolous insects. He showed how, in *Sialis*, the internal, median, longitudinal ridge is produced by the invagination of the sternum in postembryonic development, and how it evolved in the phylogenetic series from a relatively poorly developed condition in Neuroptera to a highly developed one in Hymenoptera and Lepidoptera. He observed that all the primary sternal elements, including the furcasternum and the basisternum, and the subcoxal ventropleurite are involved in the formation of the internal, median longitudinal ridge in holometabolous insects. However, Weber still thought that the basisternum is externally undefinably exposed in Hymenoptera, as is evident from his study of the tenthredinid thorax which appeared in 1927. Thus he did not apply his theory strictly to the actual morphological interpretation of the ventral areas of the thorax.

Ferris, in his series of works (Ferris and Pennebaker 1939; Ferris and Rees 1939; Rees and Ferris 1939; Ferris 1940a, 1940b), never referred to the ontogenetic formation of the median longitudinal ridge, but was consistent in regarding the ventral region of the thorax in holometabolous insects as represented by the sub-

coxal elements alone. He regarded the median longitudinal groove, where the median internal longitudinal ridge is formed, as the point of union of the subcoxae coming from both sides of the thorax, and called it the discrimen. Thus, while Weber discovered the fact of the invagination of the sternum, the emphasis placed on this invagination and the consistent application of this idea to morphological interpretation of the pleurosternal region of holometabolous insects were contributed by Ferris.

Weber and Ferris differed sharply on the question whether the invaginated sternum is the primary condition or a secondary one. For Weber it was secondary, as was indicated by his explanation of the phylogenetic development of the invagination. According to him, the furcasternum and the basisternum compose the primary sternum, and the tricondylar articulation of the pleuron with the coxa is a derived condition. Ferris, however, believed the absence of the sternum externally and the tricondylar articulation in holometabolous insects to be the primary condition, and regarded the basisternum as a secondary development in phylogeny of insects. He based his contentions chiefly on the fact that the holometabolous insects are, numerically, a great majority. Matsuda (1956a) agreed with Ferris on the ground that no dorsoventral muscles are attached on the basisternum in some primitive insects.

The idea that the basisternum is a secondarily derived condition in evolution is, however, subject to serious objections from various angles. First, the externally well-defined basisternum is present in such primitive insects as Thysanura, Ephemeroptera, and practically all hemimetabolous insects—which are more primitive, at least in their mode of postembryonic development, than the holometabolous ones. Second, as Weber (1928), with *Sialis*, and Kelsey (1957), with *Corydalis*, have shown, the sternum is clearly present in larvae and pupae, although it becomes narrower in the later stages of development, especially in the pupa. The complete invagination of the sternum apparently occurs in these insects at the final stage of development from the pupa to the adult.

There are some holometabolous insects in which the sternum is incompletely invaginated, as will be shown later in this work. Moreover, the invagination of the sternum on the median longitudinal axis is by no means peculiar to the holometabolous insects. A very similar invagination occurs also in some hemimetabolous insects, although much less pronounced than in holometabolous ones. Larsén (1945), for instance, found the median longitudinal ridge on the sternum of many species of Heteroptera, and thought this to be a more primitive condition than the more conspicuous ridge formed in Homoptera. Delamare-Debouteville (1952) has shown a phylogenetic development of this ridge[3] in a series of forms of the Blatteroidea, from the least pronounced condition in Blattaria to the most highly developed condition in Mantodea and some Isoptera.

The median longitudinal invagination of the sternum is, thus, common to all groups of pterygote insects, and the differences lie only in the degree of development. The very strong invagination in holometabolous insects appears to be associated with its peculiar way of metamorphosis at the final stage of development and some functional reasons must be involved with it, as Kelsey (1957) suspected. Although offering only indirect evidence, the literature survey by Matsuda (1958) on the origin of the external genitalia indicated that, throughout the orders of insects, the sternum occupies a considerable area on the ventral surface of the abdomen in the embryo. A similar condition probably exists in the thorax of insects. Thus it is obvious from the foregoing discussion that the weight of evidence is much heavier in favor of the orthodox view that the exposed sternum is the primary condition. Ferris' original idea, as well as the newer one of Weber (1952) discussed by Matsuda (1956a), are not accepted in the present work.

In his morphological work Weber never placed importance on the suture which Ferris called the pleural costa (precoxal suture), although he (1928) correctly identified it in *Sialis* as the one dividing the subcoxa into the anapleural (dorsal) and katapleural (ventral) rings. Since he always implicitly regarded the basisternum as present (though not specifically outlined externally) on the ventral surface of the thorax, the suture run-

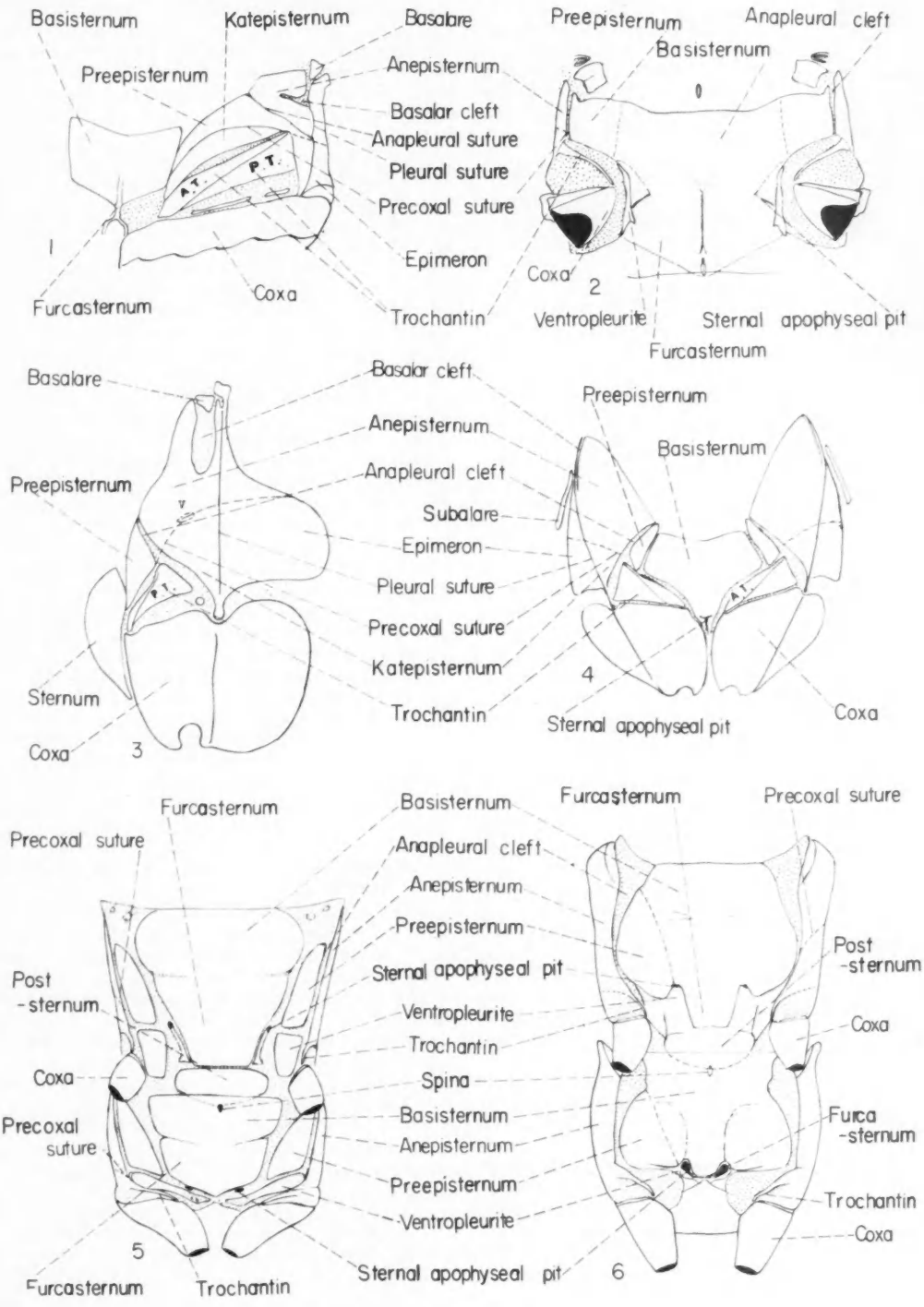
[3]This ridge has been called the sternellum by some workers.

EXPLANATION OF PLATE I

ABBREVIATIONS

Ancl. = Anapleural cleft. Anep. = Anepimeron. Anst. = Anepisternum. Ba. = Basalare. Bcl. = Basalar cleft. Bs. = Basisternum. Fs. = Furcasternum. Kast. = Katepisternum. Katep. = Katepimeron. Pls. = Pleural suture. Pres. = Preepisternum. Prs. = Precoxal suture. Troc. = Trochantin. Venp. = Ventropleurite. Broken lines indicate sutures that have been lost.

FIG. 1.—*Blattella germanica* (Linnaeus) (Blattaria), ventral view of mesothorax. FIG. 2.—*Acroneuria pacifica* Banks (Plecoptera), ventral view of mesothorax. FIG. 3.—A typical termite (Isoptera), lateral view of mesothorax (Fuller 1924). FIG. 4.—*Mastotermes darwinensis* Froggart (Isoptera), ventral view of mesothorax. FIG. 5.—*Antipaluria aequecercata* Enderlein (Embioptera), ventral view of pterothorax in wingless form. FIG. 6.—*Antipaluria aequecercata* Enderlein (Embioptera), ventral view of pterothorax of winged form.


Basisternum
Katepisternum
Basalare
Preepisternum
Anepisternum
Basalar cleft
Anapleural suture
Pleural suture
Precoxal suture
Epimeron
A.T.
P.T.
1
Furcasternum
Coxa
Trochantin
Preepisternum
Anapleural cleft
Basisternum
2
Coxa
Ventropleurite
Sternal apophyseal pit
Furcasternum
Basalare
Basalar cleft
Anepisternum
Anapleural cleft
Preepisternum
Subalare
Epimeron
Pleural suture
Precoxal suture
Katepisternum
Trochantin
P.T.
Sternum
Coxa
3
Preepisternum
Basisternum
A.T.
4
Sternal apophyseal pit
Coxa
Furcasternum
Precoxal suture
Basisternum
Anapleural cleft
Anepisternum
Preepisternum
Sternal apophyseal pit
Ventropleurite
Trochantin
Spina
Basisternum
Anepisternum
Preepisternum
Ventropleurite
Sternal apophyseal pit
Furcasternum
Precoxal suture
Post
-sternum
Coxa
Precoxal
suture
5
Furcasternum
Trochantin
6
Post
-sternum
Coxa
Furca
-sternum
Trochantin
Coxa

ning across this same area in holometabolous insects cannot, strictly, be the one merely dividing the subcoxa into the ana- and katapleural rings; it also divides the sternum. Ferris, however, paid much attention to this suture as the one which so divides the subcoxa, and its importance in this connection will be shown repeatedly in this work.

The other significant contribution by Ferris on the morphology of the pleurosternal region of the pterothorax was his calling attention to the anapleural cleft or suture, which divides the anapleural ring of the pleuron into two distinct plates, the anepisternum dorsally and the preepisternum ventrally. This cleft or suture apparently is a very persistent one, retained in almost all orders of insects. Thus it can serve as an excellent morphological landmark, as will be noted in the following discussion.

THE PRIMITIVE PLEURAL REGION OF THE PTEROTHORAX AND ITS EVOLUTION

According to Snodgrass (1927) and Weber (1928), the subcoxa, as the primitive leg segment, was a simple ring surrounding the coxal base, articulated with the latter by the anterior and posterior hinges from which, later, the anterior trochantinal and lateral (posterior) articulations, respectively, have been derived. With the incorporation of the subcoxa into the pleural membrane between the tergum and the sternum, the subcoxa acquired the pleural ridge to give a support to the wing base and the subcoxal ring, originally single, became double, with the outer, anapleural ring and the inner, katapleural ring separated by a membrane or a suture; and the subcoxal surface further split into several separate pieces or sclerites. Apart from the validity of this highly hypothetical account regarding the origin of the pleuron, the question immediately arises as to just what the primitive structural plan of the pleuron might have been.

As Snodgrass (1927) maintained, the primitive pleural region of the pterothorax must have been highly membranous, with some isolated sclerites forming two rings above the coxa, as in some groups of Apterygota and Arthropoda. It is with the acquisition of wings and its further development that the pterothorax has undergone increasing sclerotization. The process of evolution of the prothorax and that of the pterothorax thus are different. In the prothorax the overall evolutionary tendency of the pleural region has been, evidently, toward the membranization or desclerotization of the sclerites, or at least a lesser degree of sclerotization than in the pterothorax, while in the pterothorax it was toward sclerotization in originally membranous areas and the resultant formation of the sutures.[4] The sutures eventually became lost by increased sclerotization. All the sutures discussed below are regarded, therefore, as appearing in the areas that were primitively membranous.

The precoxal suture, which divides the subcoxal ring into the ana- and katapleural rings, was primitively complete, extending throughout the episternal and epimeral regions and ventrally between the coxa and the sternum (fig. 27). Although this condition is no longer recognizable in living insects, there are some primitive insects which retain the suture intact across the entire regions of the episternum and epimeron—e. g., *Sialis* (Neuroptera), *Merope* (Mecoptera), *Siphlonurus* (Ephemeroptera), *Epiophlebia* (Odonata), etc. The precoxal suture, when present in the episternal region, passes through the episternum at some distance above the trochantin, and not immediately above it. This is evidenced by the presence of either a sclerotized or a membranous area intervening between the precoxal suture and the dorsal margin of the trochantin in many primitive insects, e.g., *Pteronarcys* (Plecoptera), *Blattella* (Blattaria), *Agulla* (Neuroptera), etc. As suggested by Matsuda (1956a), the pleural abductor of the coxa, which originates along the precoxal suture, often helps to identify this suture. Some earlier workers tended to regard the trochantin as defining the upper limit of the katapleural ring of the subcoxa, but apparently this is not true. The precoxal suture has become lost in varying degrees in various insects, as will be noted in the following section of this paper. Therefore, when this suture is lost, the definitive episternum must contain the part of the katapleural element which was originally present above the trochantin, as shown by Grandi (1950) in her study on the postembryonic development of Plecoptera.

A priori it might be expected that the trochantin, if it ever existed as a sclerite on the highly membranous pleural wall of the primitive insects, must have been an isolated sclerite, articulated only anteriorly with the coxal margin.[5] The primitive, isolated trochantin is what is called the anterior trochantin, which is always articulated with the coxal margin. It is seen in Dermaptera (fig. 8), and apparently it became fused with the sclerotized katepisternal region basally in some insects (Neuroptera, Plecoptera, etc.; figs. 2, 12, 28).

In many groups of insects another sclerite, the

[4]Kelsey (1957) showed that sclerotization in ontogenetical development does not necessarily result in the formation of sutures. Thus a suture is not necessarily the seam between two sclerotized areas, as has commonly been accepted. In many cases, as the present study indicates, a primitively membranous area has become a suture in phylogeny.

[5]According to Snodgrass (1927), the trochantin primitively had two points of articulation with the coxal margin. His trochantinal sclerite in the nymph of *Perla* sp., on which his contention was based, is apparently the whole katapleural ring of the subcoxa, of which the trochantin is an apically fused part. Therefore, the posterior point of articulation with the coxa can not be regarded as a part of the trochantin.

posterior trochantin, was formed below the primitive anterior trochantin. That this is a secondary formation is convincingly evidenced by the fact that it is always the anterior trochantin, not the posterior, that is articulated with the coxal margin anteriorly, as Crampton and Hasey (1915) pointed out. The anterior and posterior trochantins are still isolated by a narrow, membranous area in the mesothorax of Dermaptera, in which the forewing is rather weakly developed and is of secondary functional importance. Both trochantins became fused in many insects and their point of fusion is indicated by an oblique suture—e.g., Blattaria, Isoptera, etc. (figs. 1, 4),—and the point of fusion (suture) is entirely obliterated by further sclerotization to form a large, definitive, single trochantin in some insects (e.g., Trichoptera, etc.; fig. 16). It should be pointed out that often it is the basal margin of the posterior trochantin that represents the basal margin of the fused, definitive trochantin. The final stage of evolution of the trochantin is the loss of articulation with the coxa and loss of independence as an isolated sclerite, due to the more advanced degree of sclerotization.

The anapleural ring of the subcoxa in primitive insects was probably composed of the anepimeron, the anepisternum, the preepisternum, and the ventropleurite. The anepisternum is defined ventrally by the membranous anapleural cleft, as is so commonly the case with primitive insects. It is retained either as a membrane or as a suture in a great many holometabolous species, though its retention is less pronounced in Hemimetabola and is completely lost in Odonata and Ephemeroptera. In primitive insects the cleft probably reached near to the anterior basal angle of the trochantin, as seen in many insects, and it has apparently become continuous with the basal margin of the trochantin in some specialized groups (e.g., Coleoptera, Hymenoptera; figs. 18, 23).

The anepisternal region in primitive insects contained a more or less vertical membranous cleft, the basalar cleft. This cleft is still retained, either as a membrane or a suture, in many Hemimetabola, although it has been lost in many species of Holometabola. The preepisternum in primitive insects probably was a plate well isolated from both the anespisternum and the ventropleurite, as seen in Plecoptera (fig. 2). The ventropleurite was a small plate located lateral to the base of the furcasternum, and in line with the preepisternum and with the postcoxal bridge on the anapleural ring of the subcoxa, as Weber (1928) indicated. The ventropleurite has had an evolutionary tendency to become fused with either the sternum or the preepisternum, or with both, or to become lost. It has never shifted around the coxa from its original ventral, and presumably anapleural, position to the anterior lateral region of the katapleural region, as some workers have thought.

Dorsal to the anapleural ring of the subcoxa two sclerites are present, one above the episternum and one above the epimeron. While the posterior one above the epimeron, the subalare, has remained in its primitive position in a great majority of insects, the basalare located above the episternum evidently has had a tendency to become approximated to the dorsal region of the anepisternum, or to become loosely attached to the inner wall of the anepisternum in some groups of insects (e.g., Neuroptera).

HOMOLOGIES

PLECOPTERA.—The pleurosternal region of the mesothorax of *Acroneuria pacifica* is shown in figure 2. The precoxal suture is partially retained (fig. 28) on the episternal region near the pleural suture. Grandi (1950) observed, in the species of Plecoptera she studied, that the dorsal part of the katepisternum becomes fused with the ventral part of the anepisternum during the course of postembryonic development, but the faint precoxal suture demarcating the anapleural and katapleural rings of the subcoxa is retained in the episternal region near the pleural suture in the two species examined (*Pteronarcys* sp. and *Acroneuria pacifica*), and apparantly also in *Chloroperla grammatica* (?) studied by Grandi (1950). In *Neoperla formosana* studied by Maki (1936), *Perla marginata* studied by Grandi (1948), and in *Perla abdominalis* studied by Wittig (1955), a pleural abductor arises along the pleural suture at its middle, where the precoxal suture is present in the other three species. The katepisternum is largely membranous, and a slender trochantin is defined by a suture basally (laterally). In the anepisternum there is apparently an indistinct basalar cleft, but the anapleural cleft is well marked and reaches the membranous area of the katepisternum near the base of the trochantin. The preepisternum and the basisternum are indistinguishably fused together in *Acroneuria pacifica*. In *Pteronarcys* sp. the preepisternal region and the basisternal regions are different in degree of pigmentation, indicating the point of fusion between the two plates. The ventropleurite is a slender plate lateral to the base of the sternal apophysis, and is clearly separated from both the basisternum and the preepisternum in both species studied in this work. The pleurosternal region of the metathorax is much the same as that of the mesothorax. The pleurosternal region of the pterothorax in Plecoptera is thus specialized in that the preepisternum and the basisternum are fused, and the precoxal suture is only partially retained in the episternal region.

BLATTARIA.—The pleurosternal region of the cockroach has been studied by various workers. Rather recent and complete works treating it were done by Crampton (1927), Carbonnell (1947), Snodgrass (1952), and Matsuda (1956a). As noted in fig. 1, the pleurosternal region of *Blattella germanica* deviates only slightly from

the hypothetical primitive plan of the pleurosternal region of the pterothorax (fig. 27). The deviations consist of the loss of the precoxal suture in the episternal region near the pleural suture and in the epimeron (indicated by a broken line). However, the complete precoxal suture extending throughout the entire pleuron was shown by Carpentier (1956) in the last-stage nymph of *Blatta orientalis*. The narrow and oblique plate, the katepisternum, superposed above the trochantin, was interpreted as the ventropleurite (laterosternite) by La Greca (1949) and Carpentier (1956). Their interpretations, however, probably are not correct. A small sclerite lateral to the furcasternum, which La Greca (1949) showed in *Blatta orientalis*, is the ventropleurite, since the position as well as the size is much like the ventropleurite occurring in such primitive forms as *Sialis* (Weber 1928a), *Corydalis* (Kelsey 1957), and Plecoptera (Weber 1928; and fig. 2). I have confirmed the presence of this plate in the same relative position in a species of *Megaloblatta*. The oblique plate above the trochantin in the cockroach is homologous to the sclerotized area of the katepisternum above the trochantin in *Agulla* (fig. 12). In the cockroach it is well differentiated as a flexible plate and is superposed above the trochantin by a membranous area, probably giving flexibility to the movement of the pleurosternal region of the thorax. Note the presence of the basalar cleft, which reaches near the upper limit of the trochantin, and also the anapleural suture which reaches the pleural suture above the base of the trochantin.

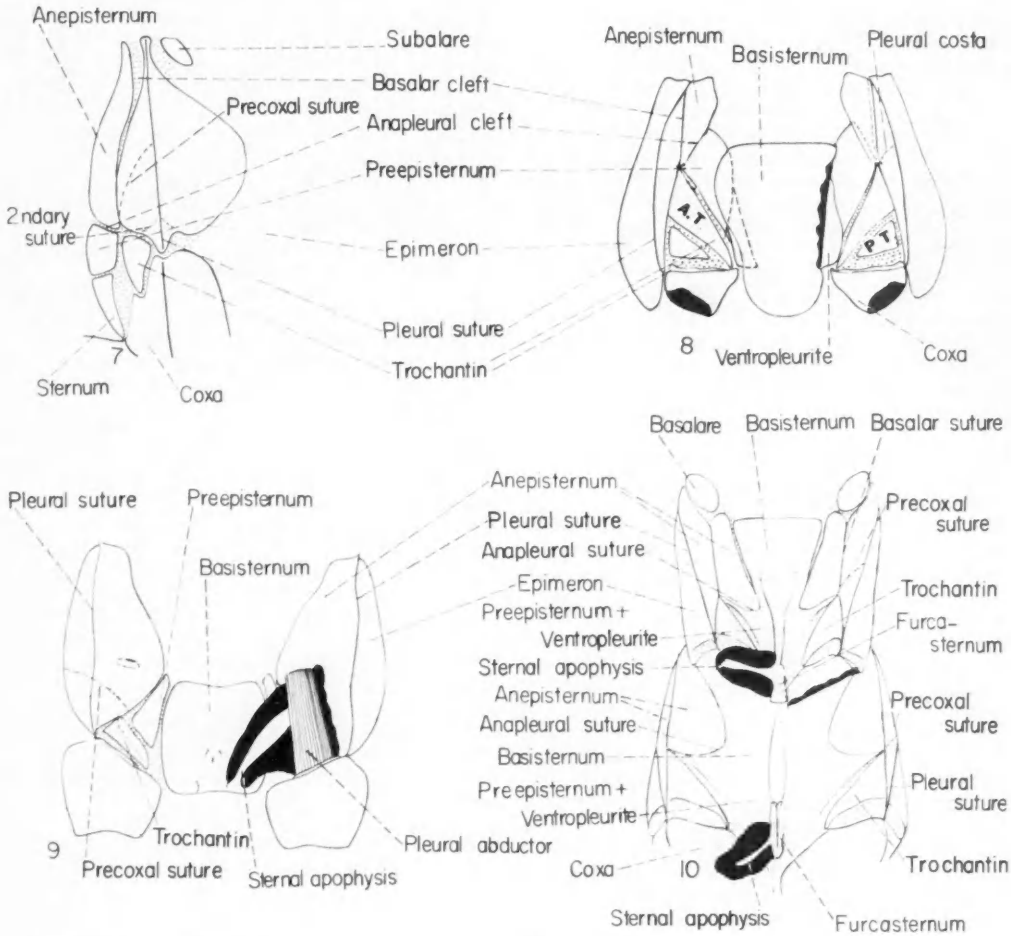
ISOPTERA.—The pleurosternal region of *Mastotermes darwinensis* is shown in figures 3 and 4. The broken line indicates the imaginary precoxal suture that must have been lost. An incomplete precoxal suture, which runs transversely across the pleural suture, apparently occurs in some Isoptera, e.g., *Zootermopsis* (Grassé 1949, La Greca 1949). Further, Fuller (1924) recognized an oval depressed spot (V in fig. 3) in *Macrotermes* and *Termes* which he regarded as dividing the mesoepisternum into the anepisternum and katepisternum. The depression falls on the imaginary suture connecting the anterobasal angle of the trochantin to the middle of the pleural suture, which usually would be the position of the precoxal suture. Thus Fuller's interpretation appears justifiable. The plate labeled preepisternum has always been called the laterosternite (ventropleurite), but it is located exactly at the position corresponding to that of the preepisternum in Blattaria and Plecoptera. If this were the ventropleurite, it would have to be lateral to the furcasternum, as in the preceding orders. The ventropleurite apparently is lost in this order. The membranous cleft bordering the preepisternum dorsally is thus regarded as the anapleural cleft. It reaches the base of the trochantin as in many other insects—e.g., *Acroneuria* (*Plecoptera*; fig. 2), *Forficula* (*Dermaptera*; fig. 8). Thus it takes no stretch of the imagination to interpret the cleft as the anapleural cleft, and the plate in question as the preepisternum. The basalar cleft is often conspicuous in Isoptera.

EMBIOPTERA.—In a large, primitive species of embiid, *Antipaluria aequecercata*, a more primitive condition of the pleurosternal region of the thorax is noted in the wingless form. The preepisternum and the ventropleurite are distinctly separated by membrane (fig. 5), and they are also separated from the sternum by a membranous area in both the meso- and the metathoracic segments. In the winged form of the same species (fig. 6) both plates are completely fused to the sternum, as will be noted by comparing figures 5 and 6. The ventropleurite is located lateral to the base of the sternal apophysis (sternal apophyseal pit), a position which it takes in other insects when present. The identification of the membranous cleft as the anapleural cleft is well justified by the fact that the cleft extends to the base of the trochantin, as in many other insects. The trochantin of the mesothorax is somewhat peculiar in that it is nearly longitudinally directed apically and its base is not well defined. The precoxal suture is completely lost in both segments, but the pleural abductor of the coxa originates from near the middle of the episternum. The broken line drawn in line with and extending toward the trochantin comes near the point of origin of the pleural abductor in both segments. The broken line, therefore, probably agrees approximately with the precoxal suture that has been lost. The anepisternum is strongly declivous along the dorsal margin in both segments. The basalar cleft is inconspicuous and the small basalar plate is present within the area of the basalar cleft. The epimeron is simple and the subalar plate is present lateral to the anterior half of the epimeron in both segments.

In the wingless form the sternal apophyseal pit is located lateral to the sternum on a thinly sclerotized, slender plate in the mesothorax, and along the posterolateral margin of the sternum in the metathorax. Because of these locations of the sternal apophyses in both segments of the wingless form and in the mesothorax of the winged form, the sternum is not divided into the

EXPLANATION OF PLATE II

FIG. 7.—A typical winged zorapteron (Zoraptera), lateral view of mesothorax (Delamare-Debouteville 1947). FIG. 8.—*Forficula* sp. (Dermaptera), ventral view of mesothorax. FIG. 9.—*Acheta assimilis* (Fabricius), ventral view of mesothorax. FIG. 10.—*Hierodula patellifera* Serville (Mantodea), ventral view of pterothorax. FIG. 11.—*Bittacus pilicornis* Westwood (Mecoptera), lateral view of pterothorax. FIG. 12.—*Agulla adnixa* (Hagen), ventral view of mesothorax.


Anepisternum
Subalare
Basalar cleft
Precoxal suture
Anapleural cleft
Preepisternum
2ndary suture
Epimeron
Pleural suture
Trochantin
7
Sternum
Coxa
Anepisternum
Basisternum
Pleural costa
A.T
P.T
8
Ventropleurite
Coxa
Pleural suture
Preepisternum
Basisternum
Trochantin
Precoxal suture
Sternal apophysis
9
Pleural abductor
Basalare
Basisternum
Basalar suture
Anepisternum
Pleural suture
Anapleural suture
Epimeron
Preepisternum +
Ventropleurite
Sternal apophysis
Anepisternum
Anapleural suture
Basisternum
Preepisternum +
Ventropleurite
Coxa
10
Precoxal suture
Trochantin
Furca-sternum
Precoxal suture
Pleural suture
Trochantin
Sternal apophysis
Furcasternum
Anepisternum
Basalare
Subalare
Anapleural cleft
Epimeron
Anepisternum
Pleural suture
Precoxal suture
Katepisternum
Trochantin
11
Coxa
Preepisternum
Preepisternum
Basalare
Spina
12
Coxa

anterior basisternum and the posterior furcasternum by a transverse ridge. In the metathorax of the winged form, however, the bases of the sternal apophyses are connected by such a ridge. The poststernite bearing the intersegmental structure, the spina, is large and well separated from the sternum proper by a narrow transverse membrane in the mesothorax of the wingless form. The poststernite in the mesothorax of the winged form is fused with the anterior metasternal region. In the wingless form of *Oligotoma japonica* the sclerotized ventropleurite is not recognized.

ZORAPTERA.—Crampton (1920b) studied the winged form of *Zorotypus hubbardi* and Delamare-Debouteville (1947) studied both winged and wingless forms of *Zorotypus guineensis*. Since the winged form of a zorapteron was not available for this study, Delamare-Debouteville's schematic drawing of the pterothorax is copied in fig. 7 and is labelled according to the interpretation and terminology used in this work. The membranous, longitudinal, basalar cleft is conspicuous, although the basalare is lacking. The preepisternum is well separated from the anepisternum by the anapleural cleft, which is continuous with the membranous area basal to the trochantin; it is also separated from the basisternum by a narrow membranous area. The ventropleurite is absent. All these features are exactly like those in Isoptera, except for the absence of the basalar plate. The ventropleurite possibly is fused with the sternum as in Embioptera. Delamare-Debouteville showed the suture defining ketepisternum and katepimeron in the metathorax (fig. 7, broken line), and regarded this as a secondary suture. This may be quite true, since the course of the suture is quite abnormal for it to be the precoxal suture. The precoxal suture is expected to be present in line with or above the dorsal margin of the trochantin, as is apparently the case in the prothorax of the species of Zoraptera which Delmare-Debouteville studied.

DERMAPTERA.—The mesothorax of *Forficula* sp. is shown in figure 8. The precoxal suture (indicated by a broken line) apparently is partially lost in the episternal region. In the katepisternal region the trochantin apparently is composed of two pieces of sclerites; only the anterior one (anterior trochantin, A.T.) is regarded as the genuine trochantin; the posterior trochantin (P.T.) is clearly separated from the anterior trochantin in this species—a condition more primitive than in Blattaria, where both plates are fused. The longitudinal suture reaching the base of trochantin in the anepisternal region is regarded as homologous with the basalar cleft, which is membranous in some hemimetabolous insects, such as cockroach or the termite. The anepisternum extends over the base of the preepisternum, thus hiding the anapleural cleft beneath. The anapleural cleft is directly continuous to the suture defining the trochantin basally; thus this interpretation is justifiable. As already noted elsewhere, the preepisternum is directly connected to the well-developed ventropleurite by an oblique suture. The ventropleurite maintains its position at the point lateral to the base of the sternal apophysis as in Plecoptera, Blattaria, etc. The sternum is excessively developed marginally, and its lateral area is superposed on the ventral area of the subcoxa. The short furcasternum is present beneath the excessively developed basisternum. The sternal apophysis is conspicuous. The spina is present at the intersegmental area between the meso- and the metasternum. The mesopleuron of the earwig is highly primitive, retaining all plates defined either by sutures or membranous clefts. Specializations are noted only in the partial loss of the precoxal suture in the episternal region and its total loss in the epimeral region, in the connection of the ventropleurite to the preepisternum by a suture, and in the loss of the basalare and subalare.

Henson (1953) studied *Forficula auricularia*. He called the anepisternum the "lateropleurite" and the ventral composite plate (ventropleurite plus preepisternum) the "laterosternite," in agreement with the terminology of Crampton[6] (1914). Henson thought that in the hypothetical primitive earwig the anapleural ring is composed of the lateropleurite and the laterosternite. However, his figure, as well as fig. 8 in this work, clearly show that his laterosternite is composed of two areas separated by an oblique suture. He failed to explain this suture, thus making his interpretation unnatural.

MANTODEA.—The ventral surface of the mesothorax in *Hierodula patellifera* (fig. 10) is remarkably similar to that of *Forficula* (Dermaptera; fig. 8). In the anapleural region the anepisternum is posteriorly well defined from the preepisternal region by the anapleural suture. Although the preepisternum and the ventropleurite are indistinguishably fused, unlike the condition in *Forficula*, the region reaches the base of the sternal apophysis as in *Forficula* or other insects. The anapleural suture reaches laterally the anterior basal angle of the trochantin as in *Forficula*. The basalar suture also runs in a very similar direction to that in *Forficula*, i.e., from the anterior margin of the anespisternum to the anterior basal angle of the trochantin. In the katapleural region the precoxal suture must have been lost from the area indicated by a broken line. The trochantin is large, its basal margin reaching laterally above the posterior point of articulation of the pleuron to the coxa. The broad basisternum is well separated from the anepisternum by a membranous narrow cleft. In the metathorax the anepisternum is not separated from the

[6]See *Terminology*.

basisternum by the membranous cleft, but by a suture. Otherwise the structural plan of the metathoracic pleurosternal region is the same as in the mesothorax.

Levereault (1937) and La Greca and Raucci (1949) showed two pieces of the basalare in *Stagmomantis carolina* and in *Mantis religiosa*, respectively. In the species studied in this work the basalare is represented by a single piece of sclerite. A peculiarity of the mantid pleurosternal region is that the basisternum extends far more anteriorly than in other orders, thus directly adjoining the anepisternum anterolaterally.

ORTHOPTERA.—In the mesothorax of *Acheta assimilis* (fig. 9), the pleurosternal region is similar to that in Isoptera. The precoxal suture is lost and its possible original position is indicated by a broken line on the episternum. The episternum is marked by a depression near the middle, indicating the point of origin of the pleural abductor of the coxa. The point of origin of the muscle probably has shifted anteriorly, accompanied by the loss of the precoxal suture. The plate labeled "preepisternum" was thought to be the laterosternite (ventropleurite) by Carpentier (1936), and was called the antecoxale by Snodgrass (1929), but it is the preepisternum in the interpretation and terminology accepted in this work. This is well justified by the fact that the anapleural cleft defining the preepisternum is continuous to the base of trochantin, as in many other insects. The ventropleurite, which should be located at the point lateral to the sternal apophysis, is not recognized. In the metathorax the preepisternum is completely fused with the basisternum, and the trochantin alone is retained as an isolated plate.

In the grasshopper, such as *Dissosteira* studied by Snodgrass (1929), the preepisternum is completely fused with the anepisternum in both the meso- and the metathorax. The ridge anterior to the trochantin of the metathorax apparently represents the true border between the basisternum and the episternum.

NEUROPTERA.—The pleurosternal region of the mesothorax of *Agulla adnixa* is shown in figure 12. The episternal region is divided into anterior and posterior halves by the distinct precoxal suture reaching the middle of the pleural suture. In the katepisternal region the basal margin of the trochantin is indistinguishably fused with the sclerotized area along the pleural suture. The anepisternum is distinguished from the preepisternum by the membranous anapleural cleft, which nearly reaches the precoxal suture. The anterior area demarcated by a broken line indicates the presence of a loosely connected process inside the wall, which Ferris and Pennebaker (1939) called the prealar apophysis. This apophysis is very probably homologous to the basalare in other insects. No trace of the basalar cleft is noted in the anepisternal region. The preepisterna meet at the median longitudinal groove, due to invagination of the sternum. There is no sternal element exposed on the ventral surface posterior to the prothoracic spina in this species. The pleurosternal region of the metathorax is very similar to that of the mesothorax.

The precoxal suture exists also in the epimeral region, dividing it into the dorsal anepimeron and the ventral katepimeron in *Sialis* sp. (Weber 1928) and in *Plega signata* (Ferris 1940a). The pleural abductor of the coxa always arises from or near the precoxal suture in all genera studied by previous workers: *Chrysopa* (Morse 1931), *Chauliodes* (Maki 1936), *Sialis* (Czihak 1954), *Palpares* (Czihak 1956), *Agulla* (Matsuda 1956a), *Corydalus* (Kelsey 1957). The ventropleurite was observed to be involved in the formation of the internal longitudinal ridge together with the sternum in *Sialis* (Weber 1928) and *Corydalus* (Kelsey 1957).

MECOPTERA.—The pleurosternal region in both the meso- and the metathorax of *Bittacus pilicornis* (fig. 11) is very similar to that in *Agulla adnixa*. The precoxal suture reaches the pleural suture much below its middle. The anapleural cleft does not quite reach the pleural suture. The basalare is separated from the anepisternum only by a narrow cleft. The basalar cleft is absent. The trochantin is small and its basal margin is lost. The sternum, as in Neuroptera, is not exposed externally on the ventral surface of the thorax and the preepisterna meet at the median longitudinal groove. The subalare is present as a well-separated plate above the epimeron.

In a very primitive species of Mecoptera, *Merope tuber*, the precoxal suture is complete, extending throughout the entire episternal and epimeral regions a little above the coxa, in both the meso- and the metathorax. In several species of *Panorpa* examined, the precoxal suture does not even reach the pleural suture. Thus the precoxal suture evidently has had a tendency to become lost, and when present in this order it is always a little above the base of the coxa. The anapleural cleft is almost entirely obliterated by sclerotization in all species of *Panorpa* examined. A thin pleural abductor of the coxa was found to originate from above the precoxal suture in a *Panorpa* sp.

DIPTERA.—Due to great reduction of the hindwing the metathorax is also greatly reduced in Diptera. A generalized pterothorax thus can be seen in the mesothorax only. In the mesothorax of *Ctenacroscelis mikado* (figs. 13, 14) the precoxal suture runs in the episternal region above the coxa and reaches the posterior point of articulation of the pleuron with the coxa. The katepisternal region, delineated anteriorly by the precoxal suture, is almost entirely membranous and is without a differentiated trochantin. The oblique suture on the episternum is regarded as equivalent to the anapleural cleft in Mecoptera.

Due to reduction of the katepisternum, the preepisternum occupies a large part of the episternum ventral to the anapleural suture and meets its counterpart from the other side of the mesothorax ventrally, forming a well-marked median longitudinal groove. The basalare is incompletely divided into two parts by a narrow cleft. The subalare is distinctly separated from the epimeral region.

The reduction of the katepisternum seems to be peculiar to Diptera and the related order Mecoptera. The reduced katepisternum is apparently present in some primitive Nematocerous flies, such as Tanyderidae and Psychoididae, as seen from the figures given by Crampton (1925, 1926). Another feature that characterizes the dipteran pleural region is its retention of the anapleural suture (or cleft). This suture apparently exists at least in a great majority of nematocerous flies, as seen from Crampton's (1925) figures. The suture called the anepisternal suture in *Tabanus atratus* by Bonhag (1949) is probably homologous with this suture.

While in the great majority of species of Diptera the sternal elements are completely invaginated into the thoracic cavity, there are some in which the sternum is well exposed externally on the ventral surface of the thorax. Crampton (1925) showed that in *Gnophomyia tristissima* (Tipulidae) there is a widely exposed sternum on the meso- and the metathorax. The same species was observed and is shown in figure 15. Its sternum is well delimited from the pleural region laterally by a longitudinal suture and is well marked by the median longitudinal groove. Because of this condition, Crampton (1925) regarded the ventral region of the thorax as the composite "pleurosternum" in cases where the longitudinal suture between the sternum and the pleuron is lost in Diptera. In *Gnophomyia tristissima* (fig. 15), however, the leg bases are so widely separated from each other in both the meso- and the metathorax that the sternum is not invaginated into the thoracic cavity. In the great majority of dipterous species, however, the leg bases approximate each other along the median longitudinal axis and the sternum is most probably completely invaginated into the thoracic cavity—as, for instance, is apparently the case with *Ctenacroscelis mikado* (fig. 13). It should be noted, however, that the sternal apopyses arise from the pits on the median longitudinal groove in the meso- and the metathorax in *Gnophomyia tristissima*. If the sternal apophysis arises from the borderline area between the sternum and pleuron in all insects, as was postulated by Weber (1927) and by Ferris and coworkers (1939–1940), the points of origin of the sternal apophyses in this species are quite abnormal. The median longitudinal ridge is conspicuous internally throughout the basisternum, furcasternum, and poststernum in the mesothorax of *Gnophyomyia tristissima*.

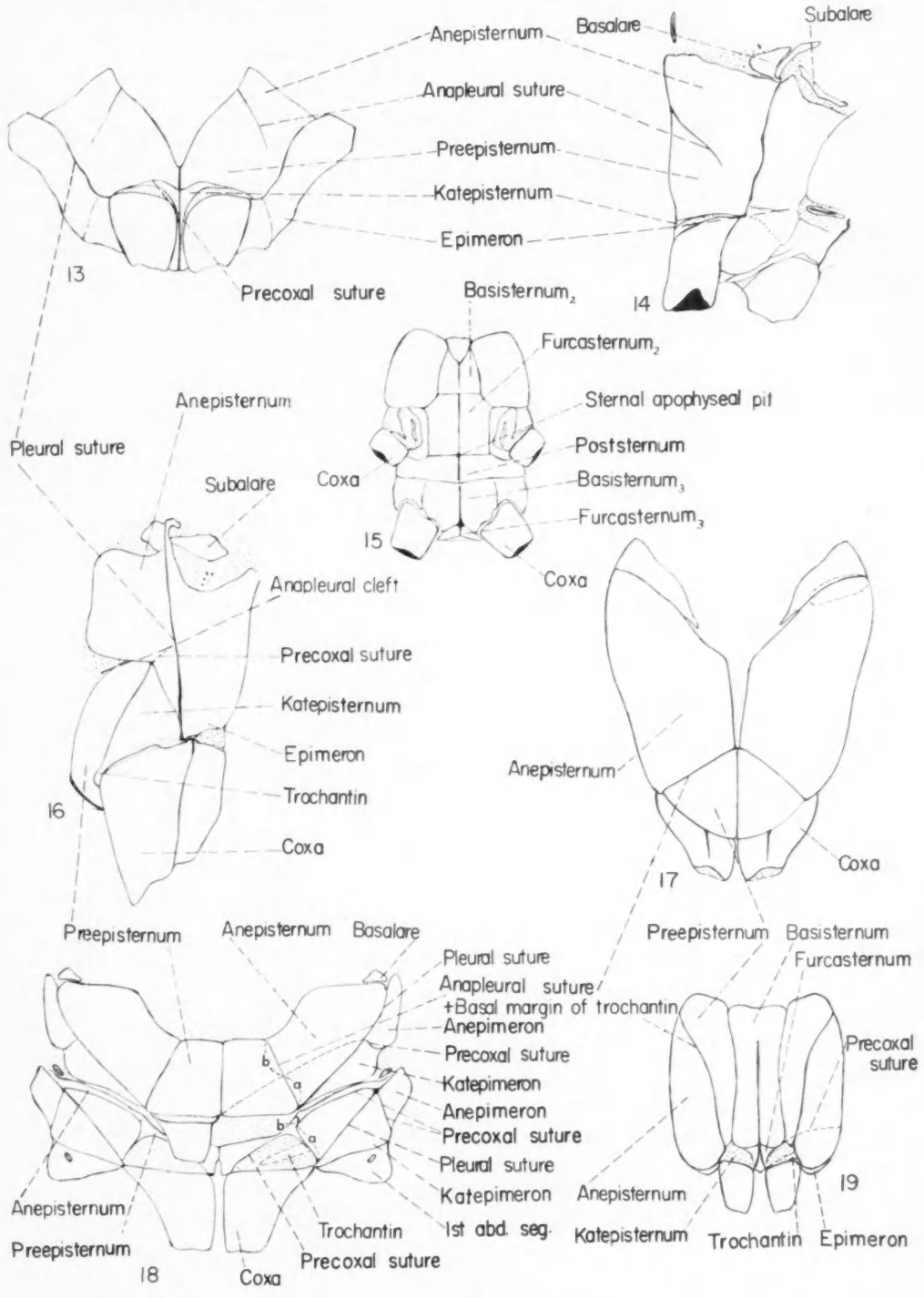
HYMENOPTERA.—The metathorax of *Arge clavicornis* (Argidae) (fig. 18), though greatly reduced, apparently retains all the primitive sutures of the katapleural ring of the subcoxa. The trochantin is lost in this species, but is retained in some other Argidae, e.g. *Schizocerus* (Weber 1927), so it is shown in the figure by a broken line. The oblique suture defining the membranous region laterally above the coxa can safely be regarded as homologous with the suture defining the trochantin in Trichoptera, Blattaria, etc. (cf. figs. 1, 16). The precoxal suture is distinct throughout the epimeral region, though it is partially lost in the episternal region. The anapleural ring of the subcoxa is so greatly reduced that the anapleural cleft (or suture) cannot be distinctly recognized, but the depressed part[7] above the oblique suture at the base of the imaginary trochantin can be the obliterated anapleural suture, and the ventral area of the anapleural ring is regarded as the preepisternum. The preepisternum meets its counterpart from the other side of the metathorax to form the median longitudinal groove. The sternum apparently is not exposed externally.

In the mesothorax the precoxal suture is retained only on the epimeron, so that the precoxal suture that has been lost in the episternal region is suggested (by a broken line) as continuing from the precoxal suture in the epimeron to the inner angle of the coxal margin, in conformity with the direction of this suture in the metathorax of this species and of other insects. The katepisternal region defined by this imaginary precoxal suture is strikingly similar in shape to that of the metathorax. The part of the oblique suture on the episternum, *a*, is apparently equivalent to the suture lateral to the trochantin in the matathorax; the part *b* is here regarded as equivalent to the anapleural cleft or suture in other insects and to the depressed area on the reduced anapleural region of the metathorax in *Arge clavi-*

[7]In *Arge similis* the depressed part is represented by a suture (Matsuda 1960), here indicated by *b*.

EXPLANATION OF PLATE III

FIG. 13.—*Ctenacroscelis mikado* Westwood (Diptera), ventral view of mesothorax. FIG. 14.—*Ctenacroscelis mikado* Westwood (Diptera), lateral view of mesothorax. FIG. 15.—*Gnohpomyia tristissima* Osten Sacken (Diptera), ventral view of pterothorax. FIG. 16.—*Arctopsyche grandis* (Banks) (Trichoptera), lateral view of mesothorax. FIG. 17.—*Xyela* sp. (Hymenoptera), ventral view of mesothorax. FIG. 18.—*Arge clavicornis* (Fabricius) (Hymenoptera), ventral view of pterothorax. FIG. 19.—*Eupelmus allynii* French (Hymenoptera), ventral view of mesothorax.


Anepisternum
Anapleural suture
Preepisternum
Katepisternum
Epimeron
Precoxal suture
13
Basalare
Subalare
14
Basisternum2
Furcasternum2
Sternal apophyseal pit
Poststernum
Basisternum3
Furcasternum3
Coxa
15
Anepisternum
Pleural suture
Subalare
Coxa
Anapleural cleft
Precoxal suture
Katepisternum
Epimeron
Trochantin
Coxa
16
Anepisternum
Coxa
17
Preepisternum
Anepisternum
Basalare
Pleural suture
Anapleural suture
+Basal margin of trochantin
Anepimeron
Precoxal suture
Katepimeron
Anepimeron
Precoxal suture
Pleural suture
Katepimeron
1st abd. seg.
Trochantin
Precoxal suture
Anepisternum
Preepisternum
18
Coxa
Preepisternum
Basisternum
Furcasternum
Precoxal suture
Anepisternum
Katepisternum
Trochantin
Epimeron
19

cornis, since the cleft (or suture) often meets or comes close to the oblique suture lateral to the trochantin (basal margin of the trochantin) in many insects—e.g., Isoptera, Dermaptera, Trichoptera, Lepidoptera, etc. (figs. 3, 4, 8, 16, 20). The suture is thus composite in origin, resulting from the fusion of the anapleural cleft (or suture) and the basal margin of the trochantin. Reference to fig. 36 will facilitate the understanding of the interpretation of this suture suggested here. It should be recalled that the oblique suture on the episternum of the mesothorax in Diptera is not composite in origin as in Hymenoptera, but is the anapleural cleft (suture) itself.

The area ventral to this composite suture in *Arge* was regarded as the sternum by Snodgrass (1910), as was the undefinably fused part of the sternum and subcoxa in Tenthredinidae by Weber (1927). The interpretation of this suture adopted in the present work, however, definitely convinces us that the area is a part of the subcoxa. The interpretations of the above-mentioned authors are apparently fallacious, since in their interpretations the coxa is articulated either with the sternum or the pleurosternum. Following the interpretation employed here, however, the coxa is articulated directly with the subcoxa, as it should be.

If the present interpretation of the suture is correct, the oblique suture in the mesothorax of *Xyela* (fig. 17) is the homologue of the corresponding oblique suture in *Arge*. The difference lies just in the degree of obliqueness of the suture between *Arge* and *Xyela*. In Xyela, due primarily to the closer approximation of the anterolateral regions of the episternum, the suture is simply a little more horizontal than in *Arge*, and the suture in *Xyela* never appears to be the one separating the sternum from the pleuron, as considered by Snodgrass (1942) and Richards (1956).

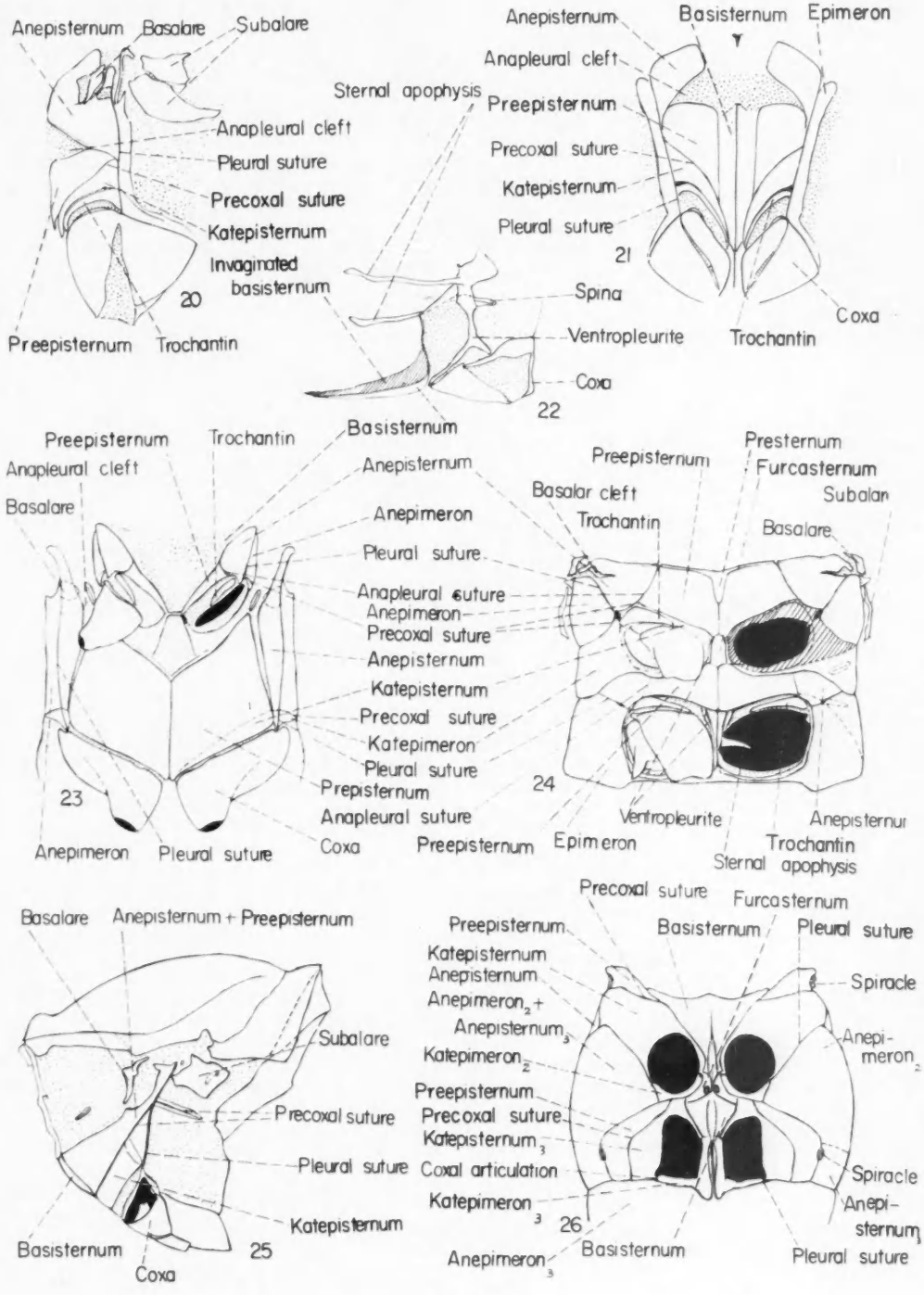
As Richards (1956) has shown, there are some hymenopterons in which the sternum is evidently exposed. In fig. 2 of Richards' work, the ventral region of the mesothorax in *Eupelmus* apparently is provided with the sternum. Closer examination of *Eupelmus allynii*, after treating by KOH, showed that there is a membranous area above the coxa (fig. 19), which Richards apparently failed to see. The course of the pleural suture in Eupelmidae is quite abnormal, greatly deviating lateroposteriorly, and a large part of the pleural suture cannot be seen in ventral view. Accompanying this abnormal course of the pleural suture the episternal region of the mesothorax is also greatly displaced posterolaterally, and the sternum is widely exposed. Because of this displacement of the episternum, the composite sutures (anapleural suture and the basal margin of the trochantin) discussed above diverge anteriorly instead of converging anteriorly as in *Arge* and *Xyela*. The suture, in spite of its abnormal course, still maintains the same position in relation to the pleural suture and reaches posteriorly near the outer coxal margin as in *Arge* and *Xyela*. It is, therefore, not the precoxal suture, as Richards (1956) interpreted it to be. The membranous area above the coxa is, by all criteria, the katepisternum, as will be immediately noted on comparison with figure 18 which shows the metathorax of *Arge clavicornis*. The trochantin and the precoxal suture that must have been lost (shown by broken lines) occur at the same position relative to the associated sutures and structures in *Arge clavicornis*. The coxa is thus directly articulated with the subcoxa, not with the sternum as Richards thought it to be in *Eupelmus*. The transverse, subtriangular area above the coxa in Richards' figure is located more ventrally and is narrower in the species of *Eupelmus* studied here. This area is obviously the furcasternum, and is not homologous to the broad subtriangular plate above the coxa in *Xyela*.

In Hymenoptera the most primitive condition of the pleural region apparently is present in the metathorax of Argidae, and this condition no longer exists in the mesothorax of any species of Hymenoptera thus far studied by various workers. The composite suture of the mesothorax discussed above apparently persists in some groups of Hymenoptera, but even this suture has been lost in many species.

TRICHOPTERA.—In the mesothorax of *Arctopsyche grandis* (fig. 16) the precoxal suture probably has been lost from the area indicated by a broken line. The katepisternal region is uniformly sclerotized over almost the entire area, and the trochantin is not differentiated as an independent plate, although its oblique basal margin is well retained near the pleural suture. The anapleural ring is divided into the anepisternum and the preepisternum by the anapleural cleft, which reaches the anterolateral end of the katepisternum. The preepisternum meets its counterpart from the other side of the mesothorax, thereby forming the median longitudinal groove

EXPLANATION OF PLATE IV

FIG. 20.—*Phassus excrescens* Butler (Lepidoptera), lateral view of mesothorax. FIG. 21.—*Phassus excrescens* Butler (Lepidoptera), ventral view of mesothorax. FIG. 22.—*Phassus excrescens* Butler (Lepidoptera), median longitudinal section of ventral part of mesothorax. FIG. 23.—*Chauliognathus marginatus* Fabricius (Coleoptera), ventral view of pterothorax. FIG. 24.—*Tibicen bifida* Davis (Hemiptera), ventral view of pterothorax. FIG. 25.—*Siphlonurus columbianus* McDunnough (Ephemeroptera), lateral view of mesothorax. FIG. 26.—*Aeschna multicolor* Hagen (Odonata), ventral view of pterothorax.


Anepisternum
Basalare
Subalare
Anapleural cleft
Pleural suture
Precoxal suture
Katepisternum
Invaginated basisternum
20
Preepisternum
Trochantin
Sternal apophysis
Anepisternum
Basisternum
Epimeron
Anapleural cleft
Preepisternum
Precoxal suture
Katepisternum
Pleural suture
21
Coxa
Trochantin
Spina
Ventropleurite
Coxa
22
Preepisternum
Trochantin
Basisternum
Anapleural cleft
Anepisternum
Basalare
Anepimeron
Pleural suture
Anapleural suture
Anepimeron
Precoxal suture
Anepisternum
Katepisternum
Precoxal suture
Katepimeron
Pleural suture
23
Prepisternum
Anapleural suture
Anepimeron
Pleural suture
Coxa
Preepisternum
Preepisternum
Presternum
Furcasternum
Basalar cleft
Subalar
Trochantin
Basalare
24
Ventropleurite
Epimeron
Anepisternum
Trochantin
Sternal apophysis
Basalare
Anepisternum + Preepisternum
Subalare
Precoxal suture
Pleural suture
Katepisternum
Basisternum
Coxa
25
Precoxal suture
Furcasternum
Preepisternum
Basisternum
Pleural suture
Katepisternum
Anepisternum
Anepimeron2+
Anepisternum3
Katepimeron2
Spiracle
Anepi-meron2
Preepisternum
Precoxal suture
Katepisternum3
Coxal articulation
Katepimeron3
26
Anepimeron3
Basisternum
Spiracle
Anepi-sternum3
Pleural suture

on the ventral surface, and the basisternum is apparently completely invaginated into the thoracic cavity. The basalare is connected with the dorsal margin of the anepisternum. The subalare is distinctly separated from the epimeron. The pleurosternal region of the metathorax is very similar to that in the mesothorax, although somewhat reduced in size.

In *Neuronia* sp. (Shepard 1930) the pleurosternal region of the mesothorax is apparently very similar to that in *Arctopysche grandis*. In these forms, however, the trochantin is apparently differentiated apically and is articulated with the coxal base. The pleurosternal region of the pterothorax probably is relatively well stabilized throughout the Trichoptera.

LEPIDOPTERA.—The pleural region of the mesothorax of a primitive moth, *Phassus excrescens* (Hepialidae) (figs. 20, 21), is very similar to that of *Agulla adnixa* (Neuroptera). The precoxal suture is entire in the episternal region, reaching near the middle of the pleural suture. In the katepisternal region the trochantin is distinctly present and is continuous directly to the pleural suture. The oblique basal margin of the trochantin apparently is lost. In the anapleural region the anepisternum is largely membranous dorsally (an expanded basalar cleft), and the basalare is present within this membranous area. The preepisternum is separated from the anepisternum by the anapleural cleft, and it is ventrally separated from the basisternum by a longitudinal suture (fig. 21). The epimeral region is largely membranous. The subalare is large and composed of two plates. The basisternum is exposed and provided with a median longitudinal groove, formed internally by invagination. The internal median longitudinal invagination of the basisternum is not conspicuous. The basisternum is quite distinct from the furcasternum and connected with it by an almost vertical ridge internally (fig. 22). The ventral process for the articulation with the coxal base is apparently formed by the ventropleurite, as Weber (1928) maintained. The apex of the ventropleurite extends close to the apex of the preepisternum as in Plecoptera. The pleural region of the metathorax is similar to that of the mesothorax. Its preepisternum is narrower and is not apically defined from the basisternum by a suture as in the mesothorax. Probably all the basisternum is invaginated to form the internal ridge. The ventral process for the articulation with the coxal base is a short, obtusely pointed process directly continuous to the median longitudinal groove beneath the furcasternum. The ventropleurite is probably invaginated, together with the furcasternum, in the metathorax.

In *Phassus excrescens* the pleurosternal region is more primitive than in the trichopterons studied in this work, in that the basisternum is exposed externally and the ventropleurite is not fused with the other part of the anapleural ring. The externally exposed basisternum was also observed in the mesothorax of *Prionoxystus robinae* (Cossidae). Crampton's (1920a) figure of *Mnemonia auricyanea* (Micropterygidae) shows a structural pattern of the pleurosternal region very similar to that of *Phassus*. Shepard's (1930) study on the pleural region of various groups of Lepidoptera, however, shows that the precoxal suture is lost wholly or partially in the episternal region of many specialized species of Lepidoptera. A rather conspicuous tendency, noted from the figures given by Shepard, is that the anapleural cleft (or suture) apparently persists at least in the great majority of the species of Lepidoptera he studied.

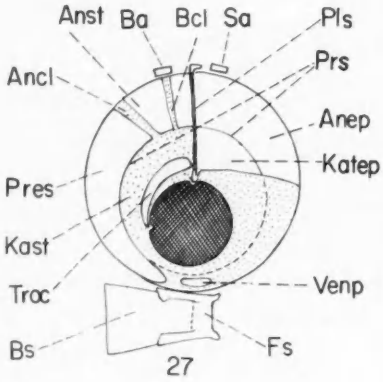
COLEOPTERA.—Unlike the condition in Hymenoptera, the metathorax is enlarged due to the presence of the primary functional wing on this segment. In *Chauliognathus marginatus* (Cantharidae, fig. 23) the mesothorax is more generalized than the metathorax in the pleural region. The precoxal suture is retained in the epimeron; it is apparently lost in the episternal region. The trochantin is distinctly retained. The anapleural region of the subcoxa is greatly reduced but is distinctly divided into the ventral preepisternum and the dorsal anepisternum by the anapleural suture. The preepisternum does not reach the median longitudinal axis of the mesothorax, and the preepisterna on the two sides of the thorax are connected by a short transverse ridge. The pleural region of the mesothorax in this species is thus remarkably similar to that of the metathorax of *Arge* (Hymenoptera; fig. 18). The basisternum is not defined anteriorly, is totally membranous, and does not form the internal ridge. The furcasternal region is also membranous, and the sternal apophysis arises from the area just below the apex of the preepisternum. The membranous region extends behind the coxa, and the sclerotized postcoxal bridge reaches the tip of the epimeron.

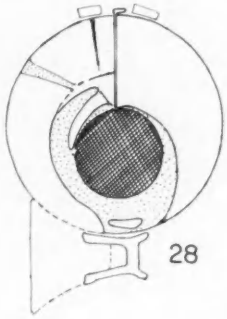
In the metathorax the precoxal suture is retained in the epimeron and partially on the episternum near the pleural suture just above the

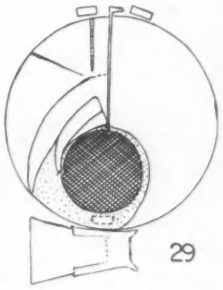
EXPLANATION OF PLATE V

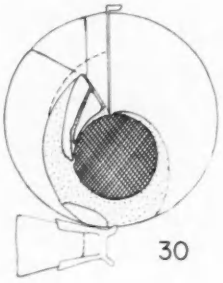
Diagrammatic drawings of the pleurosternal region of the pterothorax in various orders of insects.

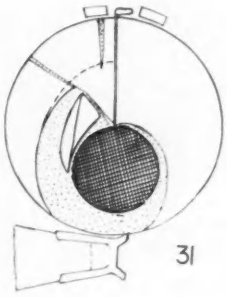
FIG. 27.—Hypothetical primitive pterothorax. FIG. 28.—Plecoptera. FIG. 29.—Blattaria. FIG. 30.—Dermaptera. FIG. 31—Isoptera. FIG. 32.—Winged Embioptera. FIG. 33.—Neuroptera. FIG. 34.—Mesothorax of Diptera. FIG. 35.—Trichoptera. FIG. 36.—Metathorax of Coleoptera and mesothorax of Hymenoptera. FIG. 37.—Odonata. FIG. 38.—Ephemeroptera.

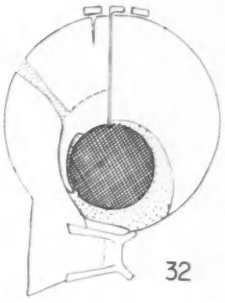

Anst
Ba
Bcl
Sa
Pls
Prs
Ancl
Anep
Katep
Pres
Kast
Troc
Venp
Bs
Fs
27

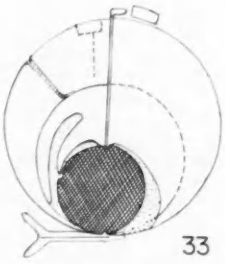

28

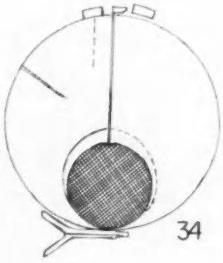

29

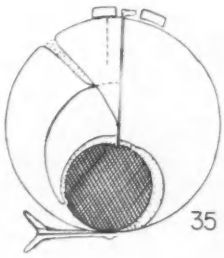

30

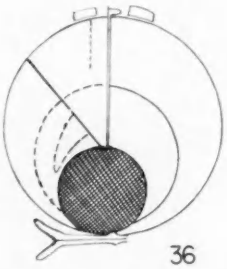

31

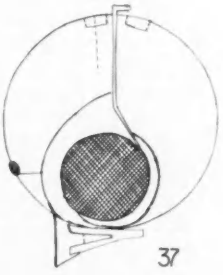

32

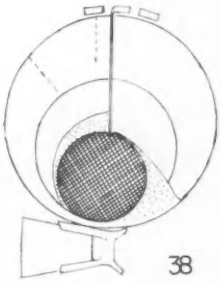

33


34


35


36


37


38

coxa. The part of the precoxal suture that has been lost in the episternal region is suggested in figure 23 by a broken line. The membranous cleft reaching the posterior point of articulation of the pleuron with the coxa is most probably the the same as the oblique suture in the mesoepisternum of Hymenoptera, i.e., the anapleural cleft plus the basal margin of the trochantin. One might get an impression of this cleft as being the composite suture resulting from the fusion of the basalar cleft and the basal margin of the trochantin, as seen in Dermaptera, because of its relatively lateral position and its nearly vertical course of direction. This interpretation, however, is definitely not correct, since the cleft arises ventral to the basalare, the point where the anapleural cleft occurs in other insects; and, moreover, the basalar cleft is seldom well developed in holometabolous insects. This composite cleft of suture apparently occurs in the metathorax of almost all groups of Coleoptera, and the cleft is often a well-marked, sclerotized groove or suture instead of the membranous cleft. The definitive preepisternum (preepisternum plus katepisternum) of one side meets that of the other side of the metathorax, and forms a well-marked, median, longitudinal groove. The sternal elements are apparently completely invaginated to form the median longitudinal ridge internally. The sternal apophyses are apparently almost completely fused, and their paired origin is indicated only apically by a median, longitudinal suture.

Campau (1939) studied *Chauliognathus pennsylvanicus*. Following Ferris' terminology, he used the name pleural costa (precoxal suture) for the mesothoracic suture which is interpreted as the anapleural suture in the present study. That interpretation is most probably not correct. The plate he labelled the katepisternum is actually the anepisternum. Campau did not show the precoxal suture (pleural costa) retained in the epimeron. The anapleural suture in the mesothorax apparently has a tendency to become lost, and the anapleural region is a simple undivided plate in the mesothorax in many species of Coleoptera, as Campau's study indicated.

HEMIPTERA.—In the mesothorax of *Tibicen bifida* (fig. 24) the precoxal suture in the episternal region runs a little above the trochantin, meets with the anapleural suture, and these together reach the conspicuous pleural apophyseal pit on the pleural suture; the precoxal suture further extends obliquely into the epimeral region from the pleural apophyseal pit, dividing the epimeron into the dorsal anepimeron and the ventral katepimeron. The epimeron is lobately produced at the posterolateral angle, covering the mesothoracic spiracle. This lobate development is apparently a secondary one. The shaded area in figure 24 is suggested to represent the original katapleural ring of the subcoxa. The anapleural region is divided into the anepisternum and the ventral preepisternum by the distinct anapleural suture. The anepisternum is provided with the inconspicuous basalar cleft and the basalare above it. The preepisternum of one side meets that of the other side of the thorax at the median longitudinal groove. The narrow ventropleurite exists along the edge of the furcasternum between the coxae. A large part of the sternum is invaginated above the median longitudinal groove, forming a robust longitudinal ridge internally. The sternum is narrowly exposed as a depressed area both anterior and posterior to the median longitudinal groove. The posterior one is the furcasternum, bearing the sternal apophyses internally, and the anterior depressed area is labelled "presternum." The pleurosternal region of this cicada is very primitive, as can be noted from the above description, and specialized features are noted only in the invagination of the basisternum and an excessive development of the posterolateral angle of the epimeron.

In the metathorax there is no precoxal suture extending laterally into the epimeral region through the pleural apophyseal pit, such as occurs in the mesothorax. The suture is suggested as being lost from the area indicated by a broken line. In the anapleural region the anepisternum is separated from the preepisternum by a rather indistinct anapleural suture. The ventropleurite is also present between the coxal bases. The basisternum is invaginated.

Taylor (1918) and Myers (1928) noted the presence of a sclerotized plate between the anepisternum and the preepisternum, where the anapleural cleft occurs, in some species of Cicadidae. As Taylor (1918) pointed out, the pleurosternal region of the cicada is remarkably similar to that of Neuroptera. Kramer's (1950) study indicates that the basic structural plan of the pleurosternal region in various groups of the auchenorhynchous Homoptera is essentially similar to that of the cicada, but certain more specialized conditions, which do not occur in the cicada, apparently occur in the other groups of the Auchenorhyncha.

In Heteroptera the overall degree of specialization of the pleurosternal region is much more advanced than in Homoptera. As already noted by Taylor (1918), the pleural suture is lost in many species of Heteroptera, thus obliterating or losing the veritable division of the episternum and epimeron. The pleural area is also excessively developed, covering the coxal base and trochantin beneath (supracoxal lobe). The supracoxal base is provided with a longitudinal cleft reaching dorsoanteriorly to the point of articulation of the coxa with the pleuron beneath. This cleft, therefore, gives a spurious impression of being the pleural suture dividing the pleuron into the episternum and epimeron. The trochantin is present beneath the supracoxal lobe in many

species of Heteroptera. Brindley (1938) concluded that the scent-gland channel is located on the precoxal suture dividing the pleuron into the ana- and katapleural rings (anterior laterale and antecoxale of Brindley) in land bugs. The thoracic scent gland, however, opens beneath the mesothoracic coxa in some aquatic Hemiptera, and the scent-gland channel runs across the metasternum to open at the middle of the metasternum (omphalium) in Gerridae and Veliidae. According to Larsén (1945), the well-isolated basalare never occurs in the mesothorax, and the primary sternum is never separated from the pleuron by the primary suture in Heteroptera.

ODONATA.—One of peculiarities of the pleurosternal region of the order Odonata is that the interpleural suture between the mesothorax and the metathorax is lost or greatly obliterated in the great majority of species, including such a primitive specieas as the *Epiophlebia superstes* studied by Asahina (1954). Due to the loss of the interpleural suture, the mesothoracic anepimeron and the metathoracic anepisternum are indistinguishably fused in *Aeschna multicolor* (fig. 26). A probable area where the suture is lost is indicated by a broken line. Another peculiarity is that the pleural suture is curved ventrad around the coxal cavity, ending near the posterolateral angle of the latter in both meso- and metathoracic segments. In line with this peculiar curvature and development of the pleural suture, the katepimeron extends ventrad to meet the katepisternum along the inner margin of the coxal cavity. The part of the precoxal suture defining the katepisternum is thus not directly continuous to the part of the same suture demarcating the katepimeron; they are connected via the pleural suture in both segments as shown in figs. 25 and 37. The katepisternum is relatively well developed and extends forward along the basisternum, and no trochantin is recognized in the katepisternal region of either segment. In the anapleural region the plate labeled preepisternum is separated from the anepisternum by the spiracle, instead of by the anapleural cleft or suture. The anapleural cleft is completely lost in Odonata. Both plates in this order, therefore, are not exactly homologous to those in other orders. The spiracle is located more dorsally in most other orders. The anapleural ring of the pleuron, due to the development of the katapleural ring along the ventral longitudinal axis of the thorax, does not reach the sternal region ventrally. Neither the basalare nor the subalare is recognized in either segment. They are represented by the internal tendonous plates in Odonata (Asahina 1954). The basisternal region is well exposed, especially anteriorly, in both segments. The furcasternum is present though narrowed in the mesothorax; that of the metathorax is believed to have been lost due to a strong compression by the extension of the katepimeron from both sides.

Asahina's (1954) description as well as his drawings of a primitive dragonfly, *Epiophlebia superstes*, indicate essential identity in the structural plan of the pleurosternal region with that of *Aeschna multicolor*, studied in this work. Asahina also has shown in the same work that the pleural abductor of the coxa arises from the precoxal suture, and the interpleural suture between the meso- and metathorax is retained only in Calopterygidae.

EPHEMEROPTERA.—A primitive species of mayfly, *Siphlonurus columbianus* (fig. 25) studied by Matsuda (1956b) shares certain peculiar features in the pleurosternal region in common with the Odonata. In both orders the anapleural cleft is lost, the trochantin is absent, and the mesothoracic spiracle occupies a more ventral position than in other orders of insects. In *Siphlonurus columbianus*, however, the pleural suture is straight, and the precoxal suture occurs much more dorsally in the epimeral region than in Odonata. The basalare as well as the subalare are well-developed, isolated plates, and the broad sternum is distinctly separated into the anterior basisternum and the posterior furcasternum by a transverse ridge.

CONCLUSIONS

Each order of pterygote insects has undergone more or less peculiar modification on the pleurosternal region of the pterothorax by fusion and loss of plates, accompanied primarily by sclerotization. These modifications are diagrammatically shown on the plates 27 to 38.

In Plecoptera (fig. 28) the modification has been realized by total loss of the precoxal suture in the epimeral region, a partial loss of the same suture in the episternal region, and incomplete or complete fusion of the preepisternum with the basisternum. In Blattaria (fig. 29) the precoxal suture is partially lost in the episternal region and totally lost in the epimeral region. The trochantin is composed of two plates, but they are demarcated by an oblique suture. In Dermaptera (fig. 30) modifications from the primitive condition are seen in the loss of the precoxal suture, and in the preepisternum being united with the ventropleurite by a suture. In Isoptera (fig. 31) the precoxal suture and the ventropleurite have apparently been completely lost. A condition similar to that in Dermaptera is noted in Gryllidae (Orthoptera). In Mantodea the ventropleurite is apparently fused with the furcasternum or with the preepisternum. In the winged form of primitive Embioptera (fig. 32) the ventropleurite is fused with the furcasternum, and the preepisternum with the basisternum; the precoxal suture is completely lost. In the winged form in Zoraptera the precoxal suture and the ventropleurite are completely lost.

In the great majority of species of the following holometabolous orders the sternum and the ventropleurite are largely invaginated into the

thoracic cavity. In Neuroptera (fig. 33) the precoxal suture is lost in the epimeral region in most species although most species retain it intact in the episternal region; the trochantin is single and its basal margin is obliterated; the basalar cleft is lost or obliterated, and the basalar plate is loosely attached to the inner wall of the anepisternum. In Mecoptera and the mesothorax of some nematocerous Diptera (fig. 34) the precoxal suture, when retained, runs a little above the coxal base, forming a narrow katepisternal region. The trochantin is inconspicuous or absent. The anapleural cleft or suture is retained either as a membranous cleft or suture in a great majority of species. In the mesothorax of some Hymenoptera and the metathorax of Coleoptera (fig. 36) the anapleural cleft has become continuous with the basal margin of the trochantin to form a nearly straight, oblique suture reaching near the point of articulation of the pleuron with the coxal base; all other sutures except for the pleural suture have been lost in the episternal region. In many species of Trichoptera (fig. 35) the precoxal suture is lost near the pleural suture in the episternal region. The katepisternal region is almost entirely sclerotized and the trochantin is represented by a large plate well demarcated basally by an oblique suture. In the related order Lepidoptera the basic structural plan is as in Trichoptera, with a more well-defined trochantin in some primitive species. In the primitive group of Hemiptera, such as Cicada (Homoptera), the basic structural plan is much the same as in Neuroptera. The precoxal suture is complete in both the episternal and epimeral regions, forming a narrow katepimeron surrounding the coxal base. In a primitive species of Ephemeroptera (fig. 38) the anapleural and basalar clefts have been lost, and the trochantin is absent. In Odonata (fig. 37) the pleural suture is curved caudad ventrally. The basalar and anapleural clefts have been lost. The definitive preepisternum is defined by the spiracle or by a suture across the spiracle. The precoxal suture is not directly continuous throughout the episternal and epimeral regions. The subalare and the basalare have become internal tendonous plates inside the pleural wall.

ACKNOWLEDGMENTS

I wish to express my appreciation to the following entomologists who have helped me during the course of this study: To Professors Kathleen C. Doering and Charles D. Michener, of the University of Kansas, for reading the manuscript. To Mr. Howell V. Daly and Saul I. Frommer, of the University of Kansas, for the discussion and criticism received. To Professors George W. Byers and Robert E. Beer, of the University of Kansas; to Professors Keizo Yasumatsu and Yoshihiro Hirashima, of the Kyushu University; to Professor Paul R. Ehrlich, of Standord University; to Professor Alfred E. Emerson, of the University of Chicago; to Dr. Edward S. Ross, of the California Academy of Sciences; to Professor Atsuo Yokoyama, of Kagoshima University; and to Professor Kenneth W. Cooper of the University of Rochester, for their gift or loan of identified specimens for study.

REFERENCES CITED

Asahina, S. 1954. A morphological study of a relic dragonfly, *Epiophlebia superstes* Selys (Odonata, Anisozygoptera). Tokyo: Japanese Society for the Promotion of Science. ix+153 pp., 71 pls.

Bonhag, P. 1949. The thoracic mechanism of the adult horsefly (Diptera: Tabanidae). Cornell Univ. Agric. Expt. Sta. Mem. 285. 39 pp., 12 pls.

Brindley, Maude D. H. 1938. The metasternum and pleuron of Heteroptera. Trans. Roy. Ent. Soc. London 82(1): 43–50, 3 pls.

Carbonell, C. 1947. The thoracic muscles of the cockroach, *Periplaneta americana* (L.). Smithsonian Misc. Coll. 107(2): 1–23, 8 pls.

Carpentier, F. 1936. Le thorax et ses appendices chez les vrais et chez les faux Gryllotalpides. Mém. Mus. Roy. Hist. Nat. Belgique (2) fasc. 4. 86 pp., 1 pl., 46 figs.

1956. Pleurites thoraciques de Lepisme et pleurites de Blatte. Ann. Soc. Ent. Belgique 91(9–10): 220–6.

Crampton, G. C. 1914. Notes on the thoracic sclerites of winged insects. Ent. News 25(1): 15–25, 1 pl.

1920a. A comparison of the external anatomy of the lower Lepidoptera and Trichoptera from the standpoint of phylogeny. Psyche 27(1): 23–34, 2 pls.

1920b. Some anatomical details of the remarkable winged zorapteron, *Zorotypus hubbardi* Caudell, with notes on its relationships. Proc. Ent. Soc. Washington 22(5): 98–106, 1 pl.

1925. Evidences of relationship indicated by the thoracic sclerites of certain eriopterine tipuloid Diptera. Insec. Inscit. Menstr. 13(10–12): 197–214, 2 pls.

1926. A phylogenetic study of the thoracic sclerites of the psychodoid Diptera, with remarks on the interrelationships of the Nematocera. Ent. News 37(2): 33–38, 65–70, 2 pls.

1927. The thoracic sclerites and wing bases of the roach *Periplaneta americana* and the basal structures of the wings of insects. Psyche 34(2): 59–72, 3 pls.

Crampton, G. C., and **W. H. Hasey.** 1915. The basal sclerites of the leg in insects. Zool. Jahrb., Abt. Anat. 39(1): 1–26, 3 pls.

Czihak, G. 1954. Beiträge zur Anatomie des Thorax von *Sialis flavilatera* L. Österreich. Zool. Zeitschr. [1953] 4(4–5): 421–48, 9 figs.

1956. Beiträge zur Anatomie des Thorax von *Ascalaphus macaronius* Scop., *Myrmeleon europaeus* McLach. und *Palpares libelluloides* Dalm. (Vergl. Anatomie des Neuropteroiden-Thorax III.). Zool. Jahrb., Abt. Anat. 75: 401–32, 13 figs.

Delamare-Deboutteville, C. 1947. Sur la morphologie des adultes aptères et ailés de Zoraptères. Ann. Sci. Nat. Zool. (11) 9: 145–54.

1952. L'homogénéité de la morphologie sternale des Blattopteroïdes (Martynov, 1938). Trans. Ninth Internatl. Congr. Ent. Amsterdam 1951, 1: 147–50, 1 pl.

Ferris, G. F. 1940a. The morphology of *Plega signata* (Hagen) (Neuroptera: Mantispidae). Microentomology 5(3): 33–56, 20 figs.

1940b. The myth of the thoracic sternites in insects. Ibid. 87–90.

Ferris, G. F., and **P. Pennebaker.** 1939. The morphology of *Agulla adnixa* (Hagen) (Neuroptera: Rhaphididae). Microentomology 4(5): 121–42, 13 figs.

Ferris, G. F., and **B. E. Rees.** 1959. The morphology of *Panorpa nuptialis* (Gerstaecker) (Mecoptera: Panorpidae). Microentomology 4(3): 79–108, 51 figs.

Fuller, C. 1924. The thorax and abdomen of winged termites. Union S. Africa Dept. Agric. [Pretoria] Mem. 2: 49–78, 3 pls., 17 figs.

Grandi, M. 1948. Contributi allo studio dei plecotteri. I. Boll. Inst. Ent. Univ. Bologna 17: 130–57, 11 figs.

1950. Contributi allo studio dei plecotteri. II. Ibid. 18: 30–57, 17 figs.

Grassé, P. P. 1949. Ordre des Isoptères ou termites. *In*: P. P. Grassé, Traité de Zoologie 9: 408–544, figs. 91–190. Paris: Masson et Cie.

Henson, H. 1953. On the external morphology of the neck and thorax in *Forficula auricularia* L. (Dermaptera). Trans. Roy. Ent. Soc. London 104(2): 25–37, 5 figs.

Heymons, R. 1899. Beiträge zur Morphologie und Entwicklungsgeschichte der Rhynchoten. Nova Acta Kais. Leopold.-Carol. Akad. Naturforsch. 74(3): 349–456, 3 pls.

Kelsey, L. P. 1957. The skeleto-motor mechanism of the dobsonfly, *Corydalus cornutus*. Part II. Pterothorax. Cornell Univ. Agric. Expt. Sta. Mem. 346. 31 pp., 11 pls. (55 figs.).

Kramer, S. 1950. The morphology and phylogeny of auchenorhynchous Homoptera (Insecta). Illinois Biol. Monogr. 20. vii+78 pp., 16 pls., 6 charts.

La Greca, M. 1949. L'evoluzione delle pleure pterotoraciche degli insetti Blattotteroidi. Boll. Zool. (Torino) 16(4–6): 119–29, 3 figs.

La Greca, M., and **A. Raucci.** 1949. Il dermascheletro e la muscolatura del torace di *Mantis religiosa*. Ann. Ist. Mus. Zool. Univ. Napoli 1(3): 1–41, 15 figs.

Larsén, O. 1945. Das thorakale Skelettmuskelsystem der Heteropteren. Ein Beitrag zur vergleichenden Morphologie des Insektenthorax. Lunds Univ. Årsk. (N.F.) Avd. 2, 41(11): 1–83.

Levereault, P. 1937. The morphology of the Carolina mantis. Univ. Kansas Sci. Bull., 1936, 24(13): 206–59, 2 pls.

Maki, T. 1936. Studies of the skeletal structure, musculature and nervous system of the alder fly *Chauliodes formosanus* Petersen. Mem. Fac. Sci. Agric. Taihoku Imper. Univ. Formosa 16(3): 117–243, 10 pls.

Matsuda, R. 1956a. The comparative morphology of the thorax of two species of insects. Microentomology 21(1): 1–65, 34 figs.

1956b. Morphology of the thoracic exoskeleton and musculature of a mayfly *Siphlonurus columbianus* McDunnough (Siphlonuridae, Ephemeroptera), a contribution to the subcoxal theory of the insect thorax. Jour. Kansas Ent. Soc. 29(3): 92–113, 8 figs.

1958. On the origin of the external genitalia of insects. Ann. Ent. Soc. America 51(1): 84–94.

1960. A new interpretation of the pleurosternal region in the pterothorax of Hymenoptera. Acta Hymenop. 1(2): 109–13.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Nat. Hist. 82(6): 157–326.

Morse, M. 1931. The external morphology of *Chrysopa perla* L. (Neuroptera: Chrysopidae). Jour. New York Ent. Soc. 39: 1–36, 4 pls.

Myers, J. G. 1928. The morphology of the Cicadidae (Homoptera). Proc. Zool. Soc. London 1928(2): 365–472, 75 figs.

Rees, B. E., and **G. F. Ferris.** 1939. The morphology of *Tipula reesi* Alexander (Diptera: Tipulidae). Microentomology 4(6): 143–78, 20 figs.

Richards, O. W. 1956. An interpretation of the ventral region of the hymenopterous thorax. Proc. Roy. Ent. Soc. London (A) 31(7–9): 99–104, 7 figs.

Roonwal, M. L. 1937. Studies on the embryology of the African migratory locust, *Locusta migratoria migratorioides* Reiche and Frm. (Orthoptera, Acrididae). II. Organogeny. Phil. Trans. Roy. Soc. London (B) 227: 175–244, 7 pls., 15 figs.

1939. Some recent advances in insect embryology, with a complete bibliography of the subject. Jour. Roy. Soc. Bengal (Sci.), Calcutta, 1938, 4: 17–105, 12 figs.

Shepard, H. 1930. The pleural and sternal sclerites of the lepidopterous thorax. Ann. Ent. Soc. America 23(2): 237–60, 6 pls., 1 fig.

Snodgrass, R. E. 1910. The thorax of the Hymenoptera. Proc. U. S. Natl. Mus. 39(1744): 37–91, 16 pls.

1927. Morphology and mechanism of the insect thorax. Smithsonian Misc. Coll. 80(1): 1–108, 44 figs.

1929. The thoracic mechanism of a grasshopper and its antecedents. Smithsonian Misc. Coll. 82(2): 1–111, 54 figs.

1935. Principles of Insect Morphology. New York: McGraw-Hill Book Co. 667 pp., 319 figs.

1942. The skeleto-muscular mechanism of the honey bee. Smithsonian Misc. Coll. 103(3): 1–120, 32 figs.

1952. A Textbook of Arthropod Anatomy. Ithaca, N. Y.: Comstock Publ. Associates. 363 pp., 88 figs.

1958. Evolution of arthropod mechanisms. Smithsonian Misc. Coll. 138(2): 1–77.

Taylor, L. H. 1918. The thoracic sclerites of Hemiptera and Heteroptera. Ann. Ent. Soc. America 23(2): 237–60, 6 pls., 1 fig.

Weber, H. 1927. Die Gliederung der Sternalregion des Tenthrediniden-Thorax. Zeitschr. wiss. Insekten-Biol. 22: 161–98, 6 pls.

1928. Die Gliederung der Sternopleuralregion des Lepidopteren-Thorax. Eine vergleichende morphologische Studie zur Subcoxaltheorie. Zeitschr. wiss. Zool. 131: 181–254, 21 figs.

1952. Morphologie, Histologie und Entwicklungsgeschichte der Articulaten. Gleichzeitig ein Bericht über Fortschritte in der Methodik der Articulatenmorphologie. Fortschr. Zool., Jena (N. F.) 9: 18–231, 43 figs.

Wittig, G. 1955. Untersuchungen am Thorax von *Perla abdominalis* Burm. (Larve und Imago) unter besonderer Berücksichtigung des peripheren Nervensystem und der Sinnesorgane. Zool. Jahrb., Abt. Anat. 74(4): 491–570, 43 figs.

SOME CHEMICAL COMPONENTS OF DROSOPHILA MELANOGASTER EGG SHELL. II. AMINO SUGARS AND ELEMENTS[1]

B. R. WILSON

Department of Entomology, Rutgers University, New Brunswick, New Jersey

ABSTRACT

Glucosamine constitutes at least 0.6 percent of the *Drosophila* egg shell. Spectrographic analysis shows the presence of 18 elements. Calcium is most abundant, followed by sodium, phosphorus and iron. Magnesium, silicon, copper, aluminum, and barium come next while boron, nickel, tin, manganese, lead, strontium, zinc, and chromium are weakly indicated.

The amino acids of *Drosophila melanogaster* egg shell were reported in a previous paper of this series (Wilson 1960). The present study deals with an investigation of the aminopolysaccharides and the elements present in the egg shell.

Aminopolysaccharides were selected for study since skeletal substances of many species of the animal kingdom, intercellular cementing agents, and a variety of biological lubricants contain such carbohydrates (Kent and Whitehouse 1955). No reference to aminopolysaccharides of insect egg shells has been found in the literature. Of interest is the work in an allied field by Brown (1955) who, in a study of the proteins of selachians and trout egg capsules reported finding 1.04 percent glucosamine. In a study of the egg envelopes of a nematode, *Cruzia americai*, Crites (1958) found that the vitelline membrane is composed of lipid material and the shell possesses chitin. This is interesting in that the reverse appears to be true in insects.

One of the difficulties accompanying investigations concerned with aminopolysaccharides has been separation of the component sugars for subsequent identification. Recently, however, ion-exchange chromatographic methods have been developed which permit the estimation of glucosamine and galactosamine with a degree of precision not possible in paper chromatography.

MATERIALS AND METHODS

The culture media used for rearing fruit flies and the procedure for the collection of shells were previously described (Wilson 1960). The procedure for the separation of amino sugars was essentially that used by Gardell (1953). Dowex 50 W 200–400 mesh X–4 (Dow Chemical Company) was washed with 4 N HCl until the washings were colorless. The cylindrical chromatographic column (0.5 x 56.5 cm.) which was dilated at the top and narrowed at the bottom, was stoppered with glass wool. The resin was added to the column and allowed to settle by gravity. When a bed of constant length was attained, the tube was connected to a reservoir containing 0.3 N HCl. The bed was then washed for 12 hours with this solution, using a flow rate of ½ to 2 ml./hr. which was maintained by raising or lowering the reservoir.

Standard solutions of glucosamine and galactosamine were prepared in 0.3 N HCl. Standard curves were constructed for these solutions by analyzing samples containing 10, 20, 50, 75, and 100 mg./0.5 ml. according to the method of Elson and Morgan (1933) as modified by Blix (1948). Readings were taken at 535 mμ in a Bausch and Lomb colorimeter.

Since it was necessary to determine the elution point of glucosamine and galactosamine from this particular column, 500 micrograms of each sugar was added, eluted and a standard recovery curve was obtained. The results appear in figure 1.

For the unknown, 80.5 mg. of *D. melanogaster* egg shells was hydrolyzed at 100° C. in 3 ml. of 6 N HCl for 9 hours. The hydrolysate was filtered and evaporated to dryness over sodium hydroxide in a vacuum dessicator. The residue was dissolved in distilled water and again evaporated to dryness. Finally, the residue was dissolved in 3 ml. of 0.3 N HCl, one-half of which was subsequently added to the column. Fractions 2 ml. in quantity were collected, using a flow rate of ½ to 2 ml. per hour of 0.3 N HCl. The results which appear in figure 2, are an average of two determinations.

The elemental analysis in table 1 was determined by using a Jarrell-Ash optical emission spectrograph. Determinations were made on each of two samples of shells which were washed thoroughly in distilled water and dried to constant weights of 23.2 and 26.2 mg. prior to volatilization. The analyses of these two samples agreed closely both qualitatively and quantitatively.

RESULTS AND DISCUSSION

A study of figure 2 reveals what appear to be three distinct peaks; the first at 50–60 ml., the second at about 88–97 ml., and the third at 97–

[1]Paper of the Journal Series, New Jersey Agricultural Experiment Station, Rutgers, The State University, Department of Entomology, New Brunswick, New Jersey. Part of a thesis presented to the Graduate Faculty of Rutgers University in partial fulfillment of the requirements for the Doctor of Philosophy degree. Accepted for publication April 21, 1960.

110 ml. of eluate. It is difficult to interpret the peak at 50–60 ml., other than to suggest the possibility that there is a compound other than glucosamine or galactosamine which is positive for the Elson-Morgan reaction.

The second peak at 88–97 ml. is interesting in that it occurs just prior to glucosamine and would appear to be a different amino sugar. Further investigation is needed however, in order to determine if this is a different sugar or if it is part of the third peak.

The peak at 97–110 ml. coincides with the elution point of glucosamine in the standard solution and is interpreted as such. This amount of hydrolyzable glucosamine constitutes approximately 0.6% by weight of the fruit fly egg shell or egg covering. The estimate may be low, however, since it was not possible to determine the amount lost due to hydrolysis.

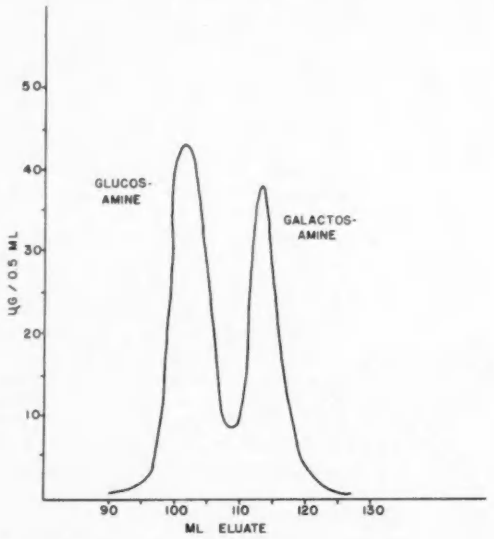


FIG. 1.—Separation of 500 μg of glucosamine and 500 μg of galactosamine on Dowex 50 ion-exchange resin.

The occurrence of glucosamine suggests that the egg shell contains an aminopolysaccharide. According to Kent and Whitehouse (1955), structural aminopolysaccharides such as hyaluronic acid, chitin, and chondroitin sulfate are found in many types of tissues where they are almost invariably associated with proteins, lipids, or both. The absence of galactosamine appears to preclude chondroitin sulfate as a possibility.

The two common aminopolysaccharides of which glucosamine is a constituent, are hyaluronic acid and chitin. Kent and Whitehouse state that "hyaluronic acid in mammals is believed to play an important part in regulating the intercellular space, as a cementing substance, and in influencing tissue permeability." In addition, capsules formed by certain microorganisms are frequently found to possess mucosubstances, e.g., hyaluronic acid, which closely resemble those of more highly developed animals. Pincus and Enzmann (1936) have described the cumulus cells in mammalian ova as being cemented together by a viscous substance. McClean and Rolands (1942), and Fekete and Duran-Reynals (1943), have suggested that this cementing substance is hyaluronic acid and that it is hydrolyzed by the action of hyaluronidase present normally in semen, thus dispersing the cumulus cells in the process of fertilization. Mutchmor and Richards (1956) have found that an extract of male gonads of *D. melanogaster* reduced the viscosity of hyaluronic acid solutions. They felt, however, that this factor was nonenzymic because it was stable to heat, dialyzable, and was not precipitated by trichloroacetic acid, in which case hyaluronidase would not seem to be indicated.

Table 1.—Semiquantitative spectrographic analysis[a] of *Drosophila melanogaster* egg covering.

Element	Probable value[b] Percent of dry weight	
Al	0.01	(0.003–0.03)
B	0.003	(0.001–0.009)
Ba	0.007	(0.002–0.021)
Ca	0.7	(0.23–2.1)
Cr	0.0004	(0.00013–0.0012)
Cu	0.03	(0.01–0.09
Fe	0.1	(0.03–0.3)
Mg	0.06	(0.02–0.18)
Mn	0.002	(0.0006–0.006)
Na	0.3	(0.1–0.9)
Ni	0.003	(0.001–0.009)
P	0.3	(0.1–0.9)
Pb	0.002	(0.0006–0.006)
Si	0.04	(0.013–0.12)
Sn	0.003	(0.001–0.009)
Sr	0.002	(0.0006–0.006)
Ti	0.001	(0.0003–0.003)
Zn	0.002	(0.0006–0.006)

[a]The author is indebted to Dr. C. L. Grant, of the Soils Department, College of Agriculture, Rutgers University, for performing this spectrochemical analysis.

[b]The figures in parentheses are limits of the accuracy of the measurements. Dr. Grant feels, on the basis of previous experience, that the probable values are very close to the actual values.

A second and more probable source of glucosamine in *D. melanogaster* egg shells is chitin. According to Wigglesworth (1950), the insect egg when laid is enclosed by two envelopes, the chorion and vitelline membrane. The chorion is the product of the follicular cells in the ovary, and the vitelline membrane originates from the cell wall of the ovum. Reports in the literature generally agree that the chorion of insect eggs does not possess chitin. Slifer (1937) stated that the vitelline membrane of the grasshopper egg

(*Melanoplus differentialis*) is chitinous, and Demerec and Kaufman (1950) referred to the vitelline membrane of *D. melanogaster* as chitinous. It was not possible in this study to separate the chorion from the vitelline membrane and, as a consequence, the analysis includes both. It is felt that in a study of the chemical constituents of the entire shell, morphological discrimination between the two membranes loses its significance. While Richards (1947) has pointed out that glucosamine is not a specific test for chitin, it is true that chitin always yields glucosamine upon hydrolysis, and it is entirely possible that a proportion of the glucosamine in *D. melanogaster* egg shells arises from chitin in the vitelline membrane.

The spectrographic analysis is an integral part of the study of the chemical composition of the egg shell, although at present it does not contribute materially to a knowledge of the combinations of elements and their function. It is felt that as the chemical structure is elucidated, it will become possible to relate the significance of these data to the overall composition of the shell.

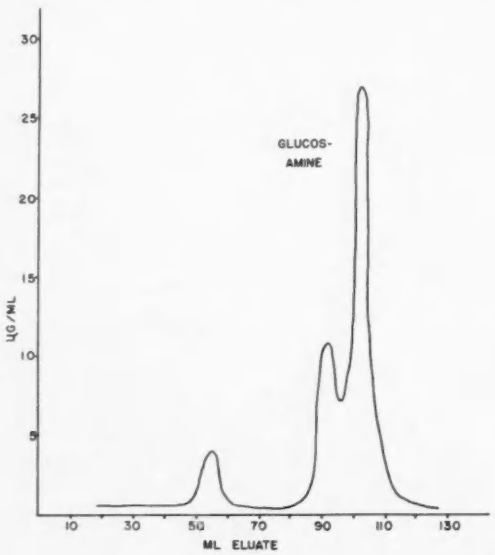


FIG. 2.—Separation and determination of glucosamine from 80.5 mg. of *Drosophila melanogaster* egg shells, using Dowex 50 ion-exchange resin.

As table 1 shows, calcium is present in the highest quantity. This is not a surprising finding since its presence in egg shells seems almost universal. In a study of the egg of the stick insect (*Bacillus libanicus*) Moscona (1950) reported that the calcium carbonate layer of the exochorion in developing eggs becomes reduced owing to loss of material from its inner surface. He subsequently determined this loss quantitatively by comparing the ash contents of shells of freshly laid and of fully developed eggs, and found the mineral content of fully developed embryos to be 12.5 times as high as the initial amount of minerals in the yolk. On this basis it was concluded that calcium carbonate was transferred from the shell into the developing embryo.

The calcium of *Drosophila melanogaster* egg shells determined here is that remaining after emergence of the embryo and unfortunately cannot be compared with the calcium content of the newly deposited egg. This large amount of calcium suggests the possibility that it is present largely as salts. According to West and Todd (1955), a number of enzymes are activated by calcium, but whether such activation is essential or even of importance to the normal metabolic processes of the embryo is not known. Zotin (1958) has studied the enzyme of salmonid eggs which sets the egg-hardening process in motion and has found that calcium ions are necessary for the activation of this enzyme. Whether a similar mechanism is responsible for the hardening process of *Drosophila melanogaster* egg shells is not known, but this finding does suggest other aspects of the fruit fly shell which should be investigated.

Sodium and phosphorus appear to be present in equivalent amounts. Salts such as CO_3 or PO_4 may be present; however, it also would be interesting to know if the phosphorus is indicative of phospho-lipid which may be present. Unfortunately it was not possible to determine potassium with this method because its only sensitivity U. V. lines lie in a region of intense cyanogen banding.

Richards (1956), in an analysis of *Sarcophaga bullota* cuticle, found at least 25 elements, but this study of the egg shell shows only 18. It would be difficult and speculative to compare the cuticle of this insect with the fruit fly egg shell. Additional comment must await further study and isolation of many compounds in order to explain more thoroughly the presence and function of these elements.

REFERENCES CITED

Blix, G. 1948. The determination of hexosamines according to Elson and Morgan. Acta Chem. Scand. 2: 467–73.

Brown, C. H. 1955. Egg capsule proteins of selachians and trout. Quart. Jour. Microsc. Sci. 96: 483–8.

Crites, J. L. 1958. The chemistry of the membrane of the egg envelope of *Cruzia americai* Maplestone, 1930 (Nematoda: Kathaniidae). Ohio Jour. Sci. 58(6): 343–6.

Demerec, M., and **B. P. Kaufman.** 1950. Drosophila Guide. Carnegie Institution of Washington. 44 pp.

Elson, L. A., and **W. T. J. Morgan.** 1933. A colorimetric method for the determination of glucosamine and chondrosamine. Biochem. Jour. 27: 1824–8.

Fekete, E., and **F. Duran-Reynals.** 1943. Hyaluronidase in the fertilization of mammalian ova. Proc. Soc. Exptl. Biol. and Med. 52: 119–21.

Gardell, S. 1953. Separation on Dowex 50 ion exchange resin of glucosamine and galactosamine and their quantitative determination. Acta Chem. Scand. 7: 207–15.

Kent, P. W., and M. W. Whitehouse. 1955. Biochemistry of the Amino Sugars. New York: Academic Press, Inc. ix+311 pp.

McClean, D., and **I. W. Rolands.** 1942. Role of hyaluronidase in fertilization. Nature 150: 627–8.

Moscona, A. 1950. Studies of the egg of *Bacillus libanicus* (Orthoptera, Phasmidae). I. The egg envelopes. II. Moisture, dry material, and minerals in the developing egg. Quart. Jour. Microsc. Sci. 91: 183–93, 195–203.

Mutchmor, J. A., and **A. G. Richards.** 1956. The degradation of hyaluronic acid by male gonads of *Drosophila*. Canadian Jour. Zool. 34: 200–5.

Pincus, G., and **E. V. Enzmann.** 1936. The comparative behavior of mammalian eggs *in vivo* and *in vitro*. II. The activation of tubal eggs. Jour. Exptl. Zool. 73: 195–208.

Richards, A. G. 1947. Studies on arthropod cuticle. I. The distribution of chitin in lepidopterous scales, and its bearing on the interpretation of arthropod cuticle. Ann. Ent. Soc. America 40: 227–40.

1956. Studies on arthropod cuticle. XII. Ash analyses and microincineration. Jour. Histochem. and Cytochem. 4: 140–52.

Slifer, E. H. 1937. The origin and fate of the membranes surrounding the grasshopper egg; together with some experiments on the source of the hatching enzyme. Quart. Jour. Microsc. Sci. 79: 493–506.

Wigglesworth, V. B. 1950. The Principles of Insect Physiology. 4th ed. New York: E. P. Dutton & Co., Inc. vii+544 pp.

Wilson, B. R. 1960. Some chemical components of the egg shell of **Drosophila melanogaster.** I. Amino acids. Ann. Ent. Soc. America 53(2): 170–3.

West, E. S., and **W. R. Todd.** 1955. Textbook of Biochemistry. New York: The Macmillan Company. xii+1,356 pp.

Zotin, A. I. 1958. The mechanism of hardening of the salmonid egg membrane after fertilization or spontaneous activation. Jour. Embryol. and Exptl. Morphol. 6(4): 546–68.

THE GENUS MICROPARSUS PATCH (APHIDAE: HOMOPTERA)[1]

CLYDE F. SMITH AND NAZIFE TUATAY[2]

ABSTRACT

This genus now contains three species, all of which commonly are found on various species of *Desmodium*. The generic type, *M. variabilis* Patch, 1909 (=*Siphonophora desmodii* Williams, 1911, n. syn.) is redescribed; its known range is from Maine and Connecticut to Iowa. New species are: *M.* **desmodiorum** (Florida to Pennsylvania and Illinois) and *M.* **olivei** (Puerto Rico to District of Columbia and Illinois).

The genus *Microparsus* was originally described by Patch (1909: 337) with *variabilis* as the type species. We have studied specimens in this genus from Canada to Puerto Rico and west as far as Illinois and Missouri. This is the known range of the genus at the present time.

The authors wish to express their appreciation to the following individuals: Dr. Roscoe E. Hill, Chairman, University of Nebraska, for the loan of Cotype slides, Nos. 133 and 135 of *Siphonaphora desmodii* Williams (equals *Microparsus variabilis* Patch); G. W. Simpson, University of Maine, for the loan of the Cotype slides of *Microparsus variabilis* Patch and aid in collecting additional material; H. H. Ross, University of Illinois, for the loan of material of *Microparsus*; J. O. Pepper, University of Pennsylvania, for the loan of material and assistance in collecting; A. N. Tissot, University of Florida, for loan of material; W. R. Richards, Canada, Department of Agriculture, for loan of material; J. B. Kring, University of Connecticut, for aid in collecting material; A. T. Olive, North Carolina State College, for aid in collecting and making some of the illustrations and photographs.

Genus **Microparsus** Patch

This genus is placed in the subtribe Pentalonina by Baker (1920: 59) because of the reduced venation in the hindwing and the fuscous bordering on the media and cubitus of the forewing. However, the general shape of the body and the frontal tubercles is characteristic of the *Macrosiphina*.

The genus is characterized as follows. Head with distinct antennal tubercles. Antennae of six segments, antennal segment III armed with subcircular sensoria. Forewings with media once branched, and with cubitus and 1st anal vein bordered with fuscous. Hindwings much reduced in size and usually lacking both media

[1]Contribution from the Department of Entomology, North Carolina State College, Raleigh. Published with the approval of the Director of Research as Paper No. 1152 of the Journal Series. Accepted for publication April 6, 1960.

[2]Miss Nazife Tuatay, entomologist from Turkey who has been studying with the senior author, 1958-59.

and cubitus. Cornicles subcylindrical. Cauda long and tapering.

KEY TO MICROPARSUS

1. Tibiae with middle portion pale, distinctly paler than distal 1/10 of tibiae; hairs on frontal tubercle blunt to slightly fan-shaped; basal 1/3–1/2 of antennal segment III pale 2
Tibiae with middle portions dark, concolorous with distal 1/10 of tibiae; hairs on frontal tubercle pointed to slightly blunt; antennal segment III black (basal 1/10 may be pale) ..... **desmodiorum** new species

2.(1) Large area around cornicle black, as dark as or darker than head or anal plate (fig. 5) ..... **olivei** new species
Small area around cornicle dusky, not distinctly darker than head or anal plate (fig. 6) ..... **variabilis** Patch

Microparsus desmodiorum, new species

Figs. 1 and 4; table 1.

Microparsus variabilis Hottes and Frison, 1931: 333 partim.

The conspicuous characteristics of this species are the black tibiae and antennae. This species was very abundant on the terminals and seed pods of *Desmodium perplexum* and *D. paniculatum*; however, it was never observed to cause any distortion of the plant as observed with *M. variabilis* and *M. olivei*. *Microparsus desmodiorum* and *M. olivei* were occasionally found on the same plant but generally the colonies were on separate plants.

Apterous Vivipara.—Color of living specimens pale yellowish-green to green, with head dark yellowish to brownish-orange and cauda yellowish to orange, legs and cornicles black; small area around cornicle dusky. Cleared specimens with head dusky, antennal segments I and II slightly darker than head but not as dark as rest of antennae, antennal segments III–VI solid black. Legs pale to slightly testaceous on coxae, trochanters, basal 3/4 to 4/5 of femora and basal 1/20 of tibiae, distal 1/5–1/3 of femora. Distal 19/20 of tibiae and tarsi black. Cornicles black. Cauda and anal plate pale, concolorous with coxae. Abdomen pale except for a dark area surrounding base of cornicle, and small dusky area around the small, lateral tubercles.

Length of hairs on vertex of head 0.023[3]; hairs on antennal III, 0.015.

Antennal III 1 with (1–4) sensoria which are very difficult to see because antennae are so dark; rostrum attaining 3rd coxae; cauda with 4 (3–4) pairs of lateral hairs plus 0 (0–3) dorsal or dorsolateral hairs.

The colonies of *desmodiorum* usually had some specimens with approximately 1/10 of the basal portion of antennal segment III pale, the basal portion of the tibiae of these specimens was lighter also; however, other distinguishing characters were not observed; therefore, we believe this to be a variation within the species.

Alate Vivipara.—Color of living specimens similar to apterous vivipara. Cleared material same as apterous vivipara except only 1/3 to 1/2 of basal portion of femora are pale and marginal sclerites are present.

Length of hairs on vertex of head 0.02, blunt; hairs on antennal III, 0.01.

Antennal III with approximately seven sensoria which are very difficult to see because the antennae are so black; rostrum attaining between 2nd and 3rd coxae; cauda with 3–5 pairs of lateral hairs plus 1–3 dorsal or dorsolateral hairs.

Apterous Ovipara.—Color of living and cleared specimens similar to apterous vivipara.

Length of hairs on vertex of head 0.025; hairs on antennal III, 0.01.

Antennal III with 0(?)–1 sensorium which is very difficult to see due to black antennae; rostrum attaining 3rd coxae; cauda with 4 pairs of lateral hairs and 3–4 dorsal or dorsolateral hairs.

Alate Male.—Color of living and cleared specimens similar to alate vivipara.

Length of hairs on vertex of head 0.02; hairs on antennal III, 0.01.

Antennal III with 18–37 sensoria; IV, 13–26; V, 9–20; rostrum attaining 2nd coxae; cauda with 3–4 pairs of lateral hairs and 3–4 dorsal or dorsolateral hairs.

Types.—Holotype in the United States National Museum. Paracolonotypes in the collection of the authors. Paratypes in the United States National Museum, and in the collections of Eastop (England), Hille Ris Lambers (Netherlands), G. F. Knowlton (Utah), Canadian National Collection (Ottawa), A. T. Olive (N. C.), J. O. Pepper (Pennsylvania), A. N. Tissot (Florida), and the authors.

Type locality.—Raleigh (Umstead Park), N. C.

Collections.[4]—On *Desmodium canadense* (L.) in Tennessee at Sugarland, August 23, 1930 (F–685–30, 5 slides, West).

On *Desmodium canescens* (L.) in Florida at Keystone Heights, June 30, 1937 (F–1551–37, 12 slides, K. V. Wheeler); Orlando, May 28, 1929 (F–532–29, 12 slides, E. West).

On Desmodium paniculatum (L.) in North Carolina at Raleigh (Umstead Park), May 19, 1959 (59–155, 1 slide); June 19, 1959 (59–327, 9 slides, Holotype and 8 Paracolonotypes, 59–330, 2 slides and 59–331, 1 slide) and at Raleigh May 25, 1959, (59–186, 5 slides); June 7, 1959 (59–305A,B,C, 13 slides); Oct. 4, 1959 (59–1306, 6 slides); North of Andrews, July 24, 1958 (58–311, 4 slides).

In Pennsylvania at Greenwood Furnace, July 30, 1959 (59–496, 1 slide, B. F. Coon, et. al.).

On Desmodium perplexum (Schub.) in North Carolina at Raleigh (Umstead Park), May 19,

[3]Measurements in millimeters, both in descriptions and in tables.

[4]Unless otherwise noted, collections were made by Mrs. Clyde F. Smith, A. T. Olive and the authors.

1959 (59–154, 2 slides); May 27, 1959 (59–214, 2 slides and 59–216, 4 slides); June 19, 1959 (59–333, 12 slides); Oct. 4, 1959 (59–1304, 6 slides) and at Raleigh, May 19, 1959 (0–59–50, 7 slides and 59–144, 1 slide); May 25, 1959 (59–185, 12 slides); June 7, 1959 (59–304A,B,C, 6 slides); Morrow Mt. State Park, July 21, 1959 (4 slides, D. A. Young); Chapel Hill, Oct. 21, 1959 (59–1404, 11 slides).

In Virginia at Arlington (Chain Bridge), Aug. 25, 1959 (59–1175, 6 slides).

On *Desmodium viridiflorum* (L.) D. C. in North

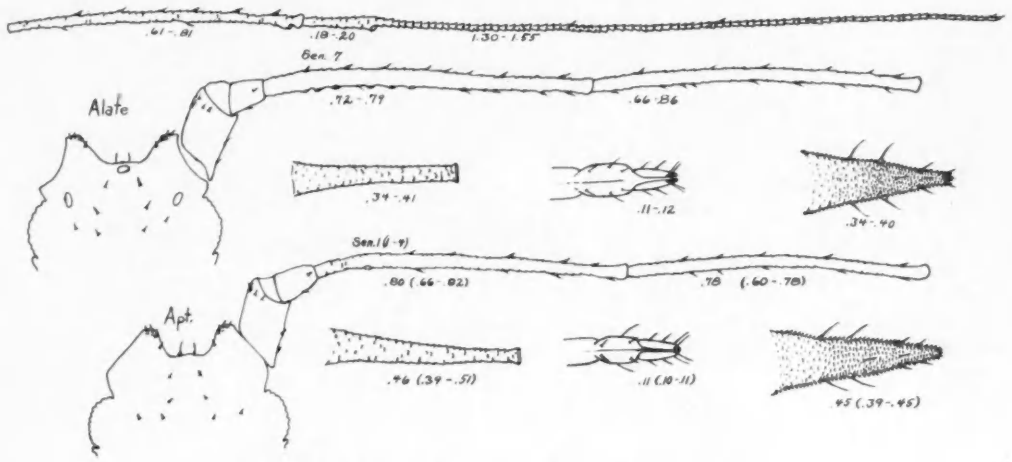


FIG. 1.—*Microparsus desmodiorum* n. sp., alate and aptera.

Table 1.—Measurements of *Microparsus desmodiorum*, specimens selected at random.

Body length	Head width	Antennae				R. IV & V		Hind tibia	Tarsus	Cornicles	Cauda length
		III	IV	V	VI	L.	W.				
Apterous viviparae											
1.54	0.44	0.66	0.60	0.54	0.15+1.10	0.10	0.06	1.71	0.11	0.39	0.39
1.49	0.45	0.71	0.63	0.58	0.15+1.18	0.10	0.04	1.90	0.11	0.43	0.41
1.74	0.45	0.82	0.75	0.65	0.18+1.28	0.11	0.04	2.04	0.11	0.44	0.43
1.98	0.49	0.80	0.74	0.63	0.18+1.30	0.11	0.06	1.98	0.11	0.51	0.44
2.00[a]	0.50	0.80	0.78	0.67	0.15+1.25	0.11	0.05	1.92	0.12	0.46	0.45
Alate viviparae											
2.03	0.46	0.79	0.67	0.66	0.19+1.36	0.12	0.06	2.02	0.10	0.36	0.36
1.76	0.46	0.72	0.71	0.72	0.19+1.30	0.11	0.04	1.97	0.11	0.34	0.34
2.06	0.47	0.78	0.79	0.77	0.18+1.49	0.11	0.04	2.01	0.11	0.36	0.35
2.27	0.50	0.79	0.86	0.81	0.19+1.55	0.12	0.05	2.16	0.12	0.41	0.40
2.02	0.47	0.77	0.79	0.68	0.20+1.50	0.11	0.04	2.02	0.11	0.38	0.37
Apterous oviparae											
1.82	0.47	0.73	0.63	0.62	0.20+1.23	0.12	0.04	1.76	0.11	0.43	0.35
1.76	0.47	0.75	0.65	0.62	0.18+1.22	0.12	0.04	1.87	0.11	0.45	0.33
2.05	0.51	0.86	0.79	0.73	0.19+1.28	0.13	0.04	2.06	0.11	0.50	0.43
2.01	0.49	0.80	0.74	0.63	0.19+1.27	0.12	0.04	1.95	0.11	0.50	0.42
2.14	0.51	0.81	0.73	0.66	0.19+1.22	0.12	0.05	1.89	0.11	0.45	0.42
Alate males											
1.93	0.44	0.61	0.61	0.55	0.14+1.10	0.12	0.05	1.78	0.10	0.23	0.20
1.76	0.42	0.59	0.58	0.52	0.14+1.12	0.11	0.04	1.62	0.10	0.22	0.21
1.73	0.47	0.64	0.64	0.55	0.15+1.17	0.11	0.04	1.67	0.10	0.21	0.20
1.94	0.46	0.74	0.72	0.69	0.15+1.34	0.12	0.05	1.86	0.11	0.24	0.25
1.92	0.45	0.68	0.65	0.62	0.12+1.25	0.11	0.04	1.78	0.11	0.23	0.23

[a]Measurements of holotype

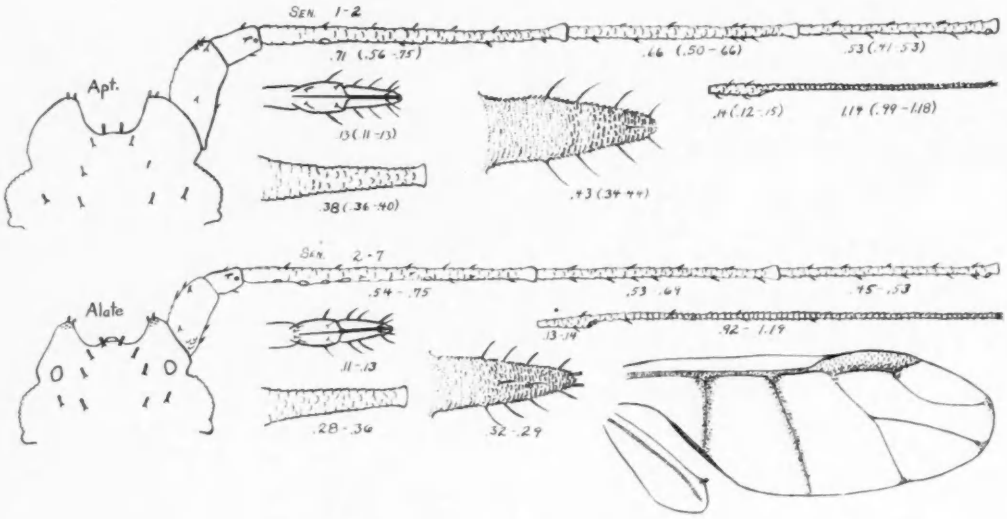


FIG. 2.—*Microparsus olivei* n. sp., alate and aptera.

Table 2.—Measurements of *Microparsus olivei*, specimens selected at random.

Body length	Head width	Antennae				R. IV & V		Hind tibia	Tarsus	Cornicles	Cauda length
		III	IV	V	VI	L.	W.				
Apterous viviparae											
1.53	0.45	0.58	0.55	0.45	0.14+0.85	0.11	0.05	1.62	0.10	0.36	0.34
1.69	0.43	0.58	0.55	0.47	0.12+0.99	0.11	0.04	1.57	0.10	0.39	0.40
1.88	0.46	0.71	0.66	0.53	0.14+1.14	0.13	0.04	1.98	0.11	0.38	0.43
1.45	0.41	0.64	0.50	0.41	0.13+1.08	0.12	0.04	1.53	0.10	0.38	0.40
1.71[a]	0.46	0.71	0.66	0.53	0.14+1.14	0.13	0.04	1.98	0.10	0.38	0.43
Alate viviparae											
1.68	0.40	0.54	0.53	0.47	0.13+0.95	0.11	0.04	1.61	0.10	0.30	0.34
1.78	0.42	0.56	0.56	0.45	0.13+0.92	0.11	0.04	1.65	0.10	0.31	0.32
1.75	0.41	0.61	0.59	0.45	0.14+1.12	0.12	0.03	1.64	0.10	0.28	0.33
1.94	0.43	0.67	0.61	0.51	0.14+1.17	0.13	0.04	1.85	0.10	0.31	0.36
2.05	0.43	0.75	0.69	0.53	0.14+1.19	0.13	0.04	1.99	0.10	0.36	0.39
Apterous oviparae											
1.91	0.46	0.71	0.60	0.54	0.13+1.08	0.11	0.05	1.78	0.11	0.37	0.34
1.82	0.44	0.74	0.63	0.56	0.13+1.04	0.11	0.04	1.78	0.11	0.38	0.35
1.84	0.44	0.72	0.66	0.56	0.14+0.99	0.11	0.04	1.77	0.11	0.37	0.33
1.81	0.45	0.75	0.60	0.54	0.14+1.07	0.12	0.05	1.74	0.10	0.39	0.34
1.84	0.43	0.71	0.64	0.57	0.12+1.08	0.11	0.04	1.72	0.11	0.36	0.33
Alate males											
1.77	0.41	0.64	0.64	0.59	0.14+1.22	0.12	0.05	1.69	0.11	0.21	0.20
1.62	0.37	0.65	0.63	0.52	0.13+1.06	0.11	0.04	1.62	0.10	0.24	0.20
1.63	0.41	0.64	0.66	0.54	0.13+1.26	0.10	0.04	1.66	0.10	0.24	0.20
1.58	0.41	0.66	0.62	0.53	0.13+1.30	0.10	0.04	1.48	0.09	0.23	0.21
1.88	0.41	0.68	0.69	0.57	0.13+1.23	0.11	0.04	1.74	0.09	0.25	0.20

[a]Measurements of holotype

Carolina at Raleigh (Umstead Park), June 19, 1959 (59–333, 1 slide and 59–335B, 5 slides).

On *Desmodium* spp. in North Carolina at Raleigh, Oct. 4, 1959 (59–1318, 3 slides) and Umstead Park, June 19, 1959 (59–332, 3 slides and 59–379, 3 slides); Oct. 13, 1959 (59–1372, 6 slides and 59–1373, 2 slides); Nov. 3, 1959 (59–1481, 1 slide) (sexuals, October-December); Chapel Hill, Oct. 13, 1959 (59–1380, 4 slides, sexuals, J. O. Pepper and C. F. Smith); Santeetlah, July 7, 1958 (58–240, 3 slides); Snowbird, July 23, 1958 (58–264, 3 slides); Richfield, Nov. 3, 1959 (59–1481, 1 slide, sexuals); Sunburst, June 19, 1941 (N. C.–27, 1 slide, A. N. Tissot and J. O.

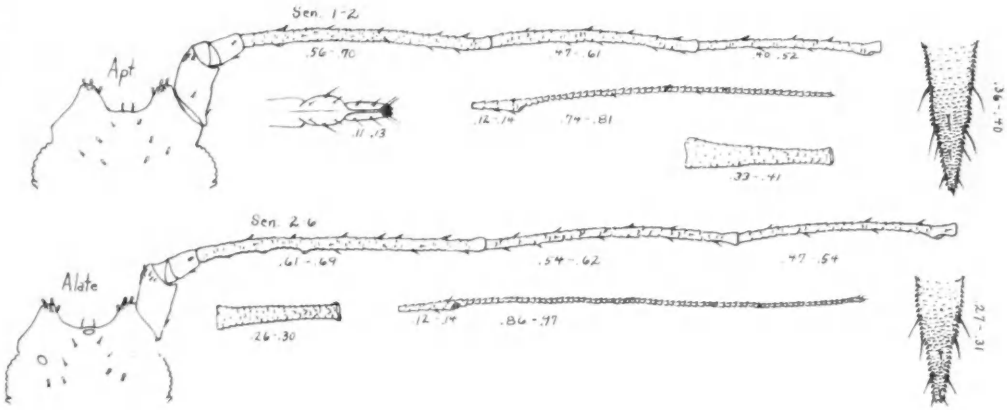


FIG. 3.—*Microparsus variabilis* Patch, alate and aptera.

Table 3.—Measurements of *Microparsus variabilis* Patch, specimens selected at random.

Body length	head width	Antennae III	IV	V	VI	R. IV & V L.	W.	Hind tibia	Tarsus	Cornicles	Cauda length
					Apterous viviparae						
2.02	0.48	0.70	0.61	0.51	0.14+0.81	0.13	0.06	1.62	0.12	0.41	0.40
1.78	0.43	0.59	0.48	0.41	0.12+0.80	0.12	0.06	1.46	0.11	0.37	0.38
1.74	0.44	0.56	0.47	0.40	0.12+0.74	0.12	0.06	1.48	0.11	0.33	0.36
1.62	0.45	0.68	0.56	0.48	0.13+0.81	0.11	0.05	1.68	0.11	0.35	0.37
1.78	0.43	0.62	0.49	0.44	0.12+0.77	0.12	0.04	1.59	0.11	0.36	0.37
					Alate viviparae						
1.90	0.42	0.61	0.56	0.49	0.13+0.95	0.12	0.05	1.60	0.11	0.27	0.27
1.78	0.40	0.69	0.62	0.52	0.13+0.94	0.12	0.05	1.74	0.11	0.28	0.30
1.66	0.40	0.65	0.54	0.47	0.14+0.86	0.12	0.04	1.74	0.11	0.30	0.30
1.65	0.42	0.69	0.62	0.53	0.14+0.97	0.11	0.04	1.81	0.10	0.30	0.30
1.91	0.42	0.61	0.54	0.54	0.12+0.92	0.12	0.05	1.74	0.10	0.26	0.31
					Apterous oviparae						
1.72	0.42	0.60	0.50	0.42	0.12+0.80	0.12	0.04	1.40	0.11	0.33	0.32
1.74	0.44	0.64	0.52	0.41	0.13+0.81	0.12	0.04	1.46	0.11	0.35	0.33
1.69	0.39	0.61	0.43	0.39	0.12+0.70	0.12	0.04	1.27	0.11	0.31	0.28
1.66	0.38	0.62	0.42	0.37	0.12+0.70	0.12	0.03	1.30	0.11	0.32	0.27
1.58	0.39	0.59	0.42	0.37	0.11+0.68	0.12	0.04	1.26	0.10	0.31	0.26
					Alate males						
1.79	0.41	0.59	0.59	0.47	0.12+0.81	0.12	0.05	1.50	0.10	0.20	0.17
1.80	0.42	0.51	0.46	0.43	0.15+0.91	0.12	0.05	1.42	0.10	0.18	0.18
1.50	0.38	0.50	0.50	0.42	0.15+ —	0.12	0.04	1.37	0.09	0.17	0.15
1.38	0.38	0.58	0.52	0.42	0.12+0.80	0.12	0.04	1.31	0.09	0.14	0.13
1.34	0.36	0.54	0.44	0.38	0.11+0.75	0.12	0.05	1.19	0.09	0.16	0.12

Pepper); Laurel Springs, Sept. 24, 1959 (59–1293, 2 slides) and Oct. 6, 1959 (59–1355, 3 slides, Chalfant and Smith).

In Florida, Parker Island, Nov. 4, 1959 (2 slides, J. O. Pepper).

In Illinois at Oakwood, Sept. 17, 1928 (51–7027, 2 slides, 51–7028, 1 slide, 51–7029, 1 slide and 51–7030, 1 slide, not types).

In Tennessee at Sugarland, Aug. 28, 1930 (F–635–30, 5 slides, E. West, not Types); Knox Co., August 7, 1918 (A1272, 1 slide); Knoxville, October 17, 1917 (1 slide); and October 26, 1918 (1385, 1 slide).

In Washington, D. C., at Zool. Park., October 24, 1911 (13854, 1 slide, and 124078, 1 slide).

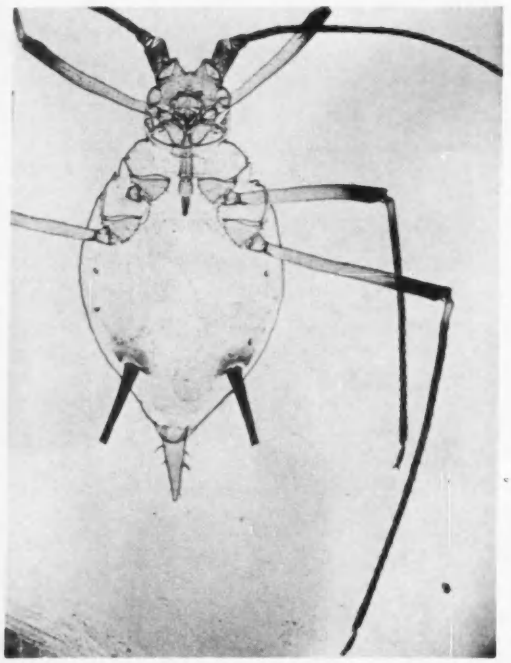


FIG. 4.—*Microparsus desmodiorum* n. sp., apterous viviparous female.

Microparsus olivei, new species

Figs. 2 and 5; table 2.

Microparsus variabilis Hottes and Frison, 1931:333, part im.

The striking characteristics of this species are the large black areas on the abdomen surrounding the chronicles and the pale areas on the tibiae. *Microparsus olivei* differs from *M. variabilis* in the area at the base of the cornicle being much larger and darker. This is very noticeable in living material as well as preserved material. The unguis of the males of *olivei* is 10–12 times the length of the hind tarsi, whereas in *variabilis* it is 7.5–9 times the length; in the ovipara the unquis of *olivei* is 9–11 times the length of the hind tarsi, whereas in *variabilis* it is 5½–7½ times the length of the hind tarsi. There is no difference in the ratios of the unguis and the hind tarsi of the apterous or the alate vivipara of *olivei* and *variabilis*.

The hairs on the antennal tubercle of *olivei* and *variabilis* are blunt to slightly fan-shaped, whereas in *desmodiorum*, new species, they are pointed to slightly blunt.

This species may cause a distortion of the terminals of *Desmodium perplexum* but has not been observed causing a distortion of other species of *Desmodium*.

This species is named in honor of A. T. Olive, who has been assisting the senior author with his aphid studies.

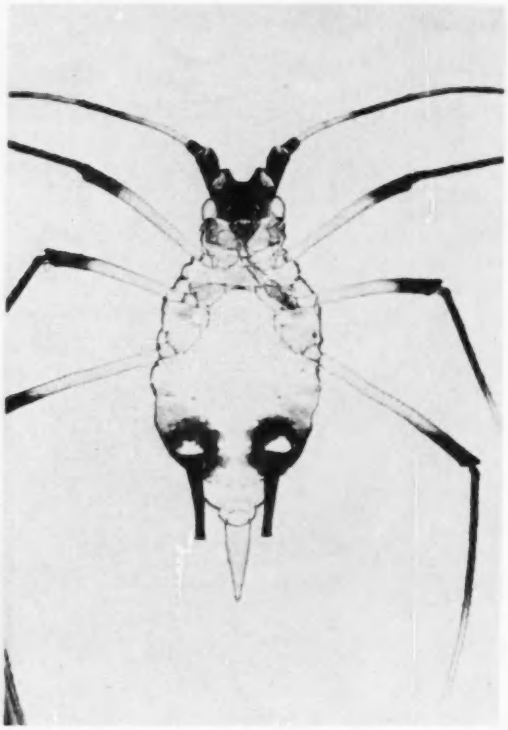


Fig. 5.—*Microparsus olivei* n. sp., apterous viviparous female.

Apterous Vivipara.—Color of living specimens dark green, with head orange to brownish and cauda orange. Cornicles black with a large, conspicuous, black area around base. Cleared material with head dark brown. Antennal segments I and II black, basal ½ of III pale, distal ½ of III and all of IV–VI black. Legs pale on all coxae, trochanters, basal ⅔–¾ of femora and middle portions of tibiae. Dark to black on distal 1/9–⅓ of femora, proximal ⅓ and distal 1/10

of tibiae and all of tarsi. Abdomen pale except large black area around cornicles and marginal sclerites. Cornicles black. Cauda and anal plate pale, concolorous with bases of femora.

Length of hairs on vertex of head 0.03; hairs on antennal III, 0.01.

Antennal III with 1 (1–2) sensoria; rostrum attaining 3rd coxae; cauda with 3 (3–4) pairs of lateral hairs and 2 (2–4) dorsal or dorsolateral hairs.

Alate Vivipara.—Color of living specimens similar to apterous vivipara. Cleared specimens similar to apterous vivipara with following exceptions: only ¼ to ⅓ of base of antennal III pale, pale area on tibiae not as pale as in aptera but the middle portion of the tibiae is distinctly paler than the ends.

Length of hairs on vertex of head 0.02; hairs on antennal III, 0.01.

Antennal III with 2–7 sensoria; rostrum attaining 3rd coxae; cauda with 3–4 pairs of lateral hairs and 2–4 dorsal or dorsolateral hairs.

Apterous Ovipara.—Color of living and cleared specimens similar to apterous vivipara, except the basal ½ of antennal segment III and the middle portion of the tibiae may be dusky.

Length of hairs on vertex of head 0.025; hairs on antennal III, 0.01.

Antennal III with 1–2 sensoria; rostrum attaining 3rd coxae; cauda with 3–5 pairs of lateral hairs and 2–3 dorsal or dorso lateral hairs.

Alate Male.—Color of living and cleared specimens similar to the alate vivipara.

Length of hairs on vertex of head 0.03; hairs on antennal III, 0.015.

Antennal III with 19–28 sensoria; IV, 14–29; V, 8–18; rostrum attaining 3rd coxae; cauda with 3–5 pairs of lateral hairs and 3–6 dorsal or dorsolateral hairs.

Types.—Holotype in the United States National Museum. Paracolonotypes in the collections of the authors and Mr. A. T. Olive. Paratypes in the U.S.N.M. and in the collections of D. Hille Ris Lambers (Netherlands), G. F. Knowlton (Utah); the Canadian National Collection (Ottawa); Olive (N. C.); J. O. Pepper (Pennsylvania); A. N. Tissot (Florida); the Agricultural Experiment Station of the University of Puerto Rico; and the authors.

Type locality.—Raleigh (Umstead Park), N. C.

Collections.[4]—On *Desmodium perplexum* (Schub.) Arlington (Chain Bridge), Va., Aug. 25, 1959 (59–1175, 6 slides).

On *Desmodium supina* in Puerto Rico at Rio Piedras, Feb. 25, 1955 (55–25, 3 slides, C. K. and C. F. Smith and L. F. Martorell); Feb. 28, 1955 (55–28, 3 slides, C. K. and C. F. Smith and Martorell); Mar. 8, 1955 (55–121, 13 slides, C. K. and C. F. Smith and Martorell); Mar. 23, 1959 (69–59, 9 slides, Martorell and Madina—Gaud).

On *Desmodium viridiflorum* (L.) in Raleigh (Umstead Park), N. C. curling leaves and terminals, June 19, 1959 (59–334, 2 slides, 59–335A, 6 slides, Holotype and Paracolonotypes).

On *Desmodium* spp. in North Carolina at Raleigh (Umstead Park), May 27, 1959 (59–218, 2 slides); June 19, 1959 (59–329, 1 slide); Sept. 2, 1959 (59–1216, 2 slides); Sept. 10, 1959 (59–1233, 3 slides); Oct. 4, 1959 (59–1316, 3 slides) and at Raleigh, July 1958 (0–58–108, 3 slides); Sept. 16, 1959 (59–1390, 6 slides); Sept. 30, 1959 (59–1299, 4 slides); Dec. 21, 1959 (1 slide); Dec. 1–10, 1959 (2 slides) (sexuals September to October); Pores Knob, Sept. 24, 1959 (59–1295, 2 slides).

FIG. 6.—*Microparsus variabilis* Patch, apterous viviparous female.

In Florida at Highlands Hammock State Park, Nov. 10, 1959 (4 slides, J. O. Pepper); Gainesville, Mar. 24, 1937 (F-1481–37, 3 slides, Harriet Foster); June 19, 1939 (F–1816–39, 2 slides, A. N. Tissot); and June 21, 1939 (F–1822–39, 1 slide, F–1826–39, 1 slide, Tissot); Palmetto, May 9, 1948 (F–3014–48, 7 slides, Tissot).

In South Carolina at Easley, Oct. 20, 1959 (7 slides, Pepper); Clemson, Oct. 18, 1927 (F–275–27, 4 slides, Tissot).

In Illinois at Edwardsville, Sept. 11, 1929 (51–7930, 4 slides, Frison and Ross).

Specimens collected on "Bush Clover" at Glennville, N. C., Aug. 8, 1957 and Hiawassee,

Georgia, Aug. 19, 1957 (W. B. Richards) are very similar to *olivei* but the cornicles are shorter and broader, therefore, these specimens are not included in the "Type" series.

Microparsus variabilis Patch, 1909

Figs. 3 and 6; table 3.

Siphonophora desmodii Williams, 1891: 6; nomen nudum.
Macrosiphum desmodii Sanborn, 1906: 237, list; nomen nudum.
Microparsus variabilis Patch, 1909: 338, desc. and figs., al., apt. and male.
Siphonophora desmodii Williams, 1911: 160(26), desc. apt. and al.
Microparsus variabilis Hottes and Frison, 1931: 333, partim.
Siphonophora desmodii Muma, 1952: 11, list.

The conspicuous characteristics of this species are the pale areas in the middle of the tibiae, the pale basal area on antennal segment III and the relatively small, dusky area around the cornicle.

Apterous Vivipara.—Color of living specimens green, head and cauda yellow to orange, cauda darker than head. Cornicles black, surrounded by a small, dusky area. Nymphs and teneral aptera yellowish to pale green. Cleared specimens with head dusky. Antennal segments I and II dusky, slightly darker than head; segment III pale on basal $\frac{2}{3}$–$\frac{3}{5}$; dark on distal $\frac{2}{5}$–$\frac{1}{3}$ of segment III, all of segments IV, V and VI. Legs pale except distal $\frac{1}{5}$ of femora, small area on proximal end of tibiae, distal $\frac{1}{10}$ of tibiae and all of tarsi which are dusky to black. (The area on the proximal end of tibiae may be concolorous with middle portion of tibiae.) Cornicles black, base often appears slightly lighter than distal half. Cauda and anal plate pale to slightly yellowish.

Length of hairs on vertex of head 0.035; hairs on antennal III, 0.013.

Antennal III with 1–2 sensoria; rostrum attaining 3rd coxae; cauda with 4 to 5 pairs of lateral hairs plus 0–4 dorsal or dorsolateral hairs.

Alate Vivipara.—Color of living specimens similar to apterous vivipara. Cleared specimens similar to apterous vivipara with the following exception: antennal segment III pale on basal $\frac{1}{4}$ to $\frac{1}{3}$.

Length of hairs on vertex of head 0.025; hairs on antennal III, 0.01.

Antennal III with 2–6 sensoria; rostrum attaining 3rd coxae; cauda with 3–4 pairs of lateral hairs, and 2–4 dorsal or dorsolateral hairs.

Apterous Ovipara.—Color of living and cleared specimens similar to apterous vivipara.

Length of hairs on vertex of head 0.027; hairs on antennal III, 0.01.

Antennal III with 1 sensorium; rostrum attaining 3rd coxae; cauda with 4–5 pairs of lateral hairs, and 3–4 dorsal or dorsolateral hairs.

Alate Male.—Color of living and cleared specimens similar to alate vivipara.

Length of hairs on vertex of head 0.03; hairs on antennal III, 0.02.

Antennal III with 16–27 sensoria; IV, 13–26; V, 7–14; rostrum attaining 3rd coxae; cauda with 3–4 pairs of lateral hairs, and 1–3 dorsal or dorsolateral hairs.

Type.—The writers have selected a lectotype from one of the original cotype series of slides. The slide bears the labels "No. 112–06, *Desmodium canadense*, Veazie, Me., 1906." The slide is in the U. S. National Museum; other slides of the original cotype series are in the collections of the Maine Agricultural Experiment Station, the U. S. National Museum, and the senior author.

Type Locality.—Veazie, Maine.

Collections.—On *Desmodium canadense* (L.) in Maine at Orono, July 31, 1925 (487–25, 3 slides and 488–25, 1 slide); Aug. 30, 1908 (56–08, 8 cotype slides); Veazie, 1906 (112–06, 7 cotype slides) and Aug. 15, 1959 (59–932, 15 slides and 59–933, 36 slides 1 male, 2 ovipara).

In Connecticut at Wallingford, Aug. 20, 1959 (59–1144, 3 slides, J. B. Kring, et. al.).

In Iowa at Ames, July 2, 1924 (51–5470, 1 slide, F. C. Hottes).

On *Desmodium canescens* (L.) West Point, July 29, 1890 (slide No. 133 labeled cotype *Siphonaphoron desmodii*) and slide No. 135 labeled *S. desmodii* Aug. 19, 1893, no locality data.

On *Desmodium* spp. in Ohio at Columbus, Aug. 24, 1959 (59–1209, 4 slides and 59–1210, 8 slides, 2 males).

In Illinois at Mattoon, Sept. 10, 1929 (51–7924, 1 slide, 51–7925, 1 slide, 51–7926, 1 slide, and 51–7929, 1 slide) and Charleston, Aug. 24, 1910 (51–5466, 1 slide, 51–5467, 1 slide).

REFERENCES CITED

Baker, A. C. 1920. Generic classification of the hemipterous family Aphididae. U. S. Dept. Agric. Bull. 826: 1–109.

Hottes, F. C., and **T. H. Frison.** 1931. The plant lice or Aphidae of Illinois. Bull. Illinois Nat. Hist. Surv. 19(3): 119–447.

Muma, M. H. 1952. Insect types in the collections of the University of Nebraska State Museum. Bull. Univ. Nebraska State Mus. 3(8): 1–35.

Patch, Edith M. 1909. The *Desmodium* aphid, *Microparsus variabilis* n. sp. Ent. News 20(8): 337–41.

Sanborn, C. E. 1904. Kansas Aphididae with catalogue of North American Aphididae and host plant and plant-host list. Univ. Kansas Sci. Bull. 3(1): 3–82, pls. 1–22.

1906. Kansas Aphididae. Part II. Ibid. 3(8): 225–75.

Williams, T. A. 1891. Host plant list of North American Aphididae. Univ. Nebraska Special Bull. 1: 1–28.

1911. The Aphididae of Nebraska. University [of Nebraska] Studies 10(2): 85–175 (1–91).

OBSERVATIONS ON THE SUBGENUS ARGAS (IXODOIDEA, ARGASIDAE, ARGAS).

3. A BIOLOGICAL AND SYSTEMATIC STUDY OF A. REFLEXUS HERMANNI AUDOUIN, 1827 (REVALIDATED), THE AFRICAN BIRD ARGASID[1]

HARRY HOOGSTRAAL[2] AND GLEN M. KOHLS[3]

ABSTRACT

Argas r. reflexus (Fabricius, 1794), recently redescribed by the writers, parasitizes wild and domestic birds in western Europe. The subspecies *hermanni* Audouin, 1827, common in Egypt and certain areas of French West Africa, is also recorded from Kenya and Sudan and may occur in Ethiopia. It infests domestic pigeons and a variety of wild birds; domestic chickens appear to be exceptional as hosts in Egypt but not uncommon in French West Africa. In Egypt, "domestic" demes of morphologically, mostly uniform individuals of *hermanni* inhabit the cool, sheltered, mudbrick interiors of numerous pigeon lofts, in which they find a constant source of food. "Feral" demes of morphologically more variable individuals infesting wild-bird nests and retreats are subject to temperature and humidity extremes, thus bloodmeals in these situations may be more infrequent or confined to the host's nesting season. An Egyptian neotype is selected for the subspecies *hermanni*, which was originally described from Egypt. Larval criteria are especially distinct for the African subspecies, as they also are for the American species *A. cooleyi* Kohls and Hoogstraal, 1960. The two Old World forms are considered as subspecies owing to almost exclusively allopatric distribution of each, the finding of a single typical larva of *A. r. reflexus* in Egypt, the presence of a few intermediate adults in both European and Egyptian samples, and the distinct possibility that both forms may be carried intercontinentally by migrating birds and may interbreed with local populations.

Larvae of *Argas* (*Argas*) from wild birds, often damaged, worn, or variously distended, may be difficult to differentiate; this is especially true of *A. r. hermanni* and *A. persicus* (Oken, 1818). Therefore, for both practical and academic interests, the larvae of *A. persicus* is described in detail and compared with other known larvae in this subgenus. West Nile virus, which causes a febrile illness in man and pigeons, has been isolated from *A. r. hermanni* during winter, thus suggesting the possibility that this tick may be an important reservoir and vector. Other viruses pathogenic for human beings have also been isolated from this tick in Egypt.

In previous reports in this series, *Argas* (*A.*) *r. reflexus* (Fabricius, 1794) of western Europe was redescribed (Hoogstraal and Kohls 1960) and *A.* (*A.*) *cooleyi* (Kohls and Hoogstraal 1960) of western North America was described. In the present study, the name *hermanni* Audouin, 1827, is resurrected for populations of bird parasites from Egypt, French West Africa, Sudan, Kenya, and (probably) Ethiopia. African populations are considered a subspecies of *A.* (*A.*) *reflexus* owing to the almost exclusively allopatric distribution of European and African forms, the finding of a single larva of *A.* (*A.*) *r. reflexus* in Egypt with nearly typical *hermanni* nymphs and adults, the presence of a few intermediate adults in both European and Egyptian samples, and the distinct possibility that both forms may be carried intercontinentally by migrating birds and may interbreed with local populations.

Special attention is called to morphological and biological differences between "domestic" demes in sheltered pigeon houses and "feral" demes in exposed, more or less infrequently occupied wild bird nests, as well as to apparently variable host-parasite relationships in Africa and to criteria for differentiating larvae of this subgenus, including that of *A.* (*A.*) *persicus*, which is redescribed in detail.

Argas (Argas) reflexus hermanni Audouin, 1827

The African Bird Argasid

(Figures 1 to 26)

REDESCRIPTION.—*Female* (figs. 2–5, 9, 10): Measures from 3.7 mm. to 6.4 mm. in length and from 2.2 mm. to 4.1 mm. in width; average specimen from pigeon houses 6.0 mm. in length and 3.6 mm. in width; average specimen from wild bird nests 4.1 mm. in length and 2.6 mm. in width. Body when unengorged as in *A. r. reflexus* (cf. Hoogstraal and Kohls 1960) except that it is smaller and usually narrower, the posterior margin is not so bluntly rounded, and the lateral margins converge very slightly less acutely (see VARIATION below).

Dorsal and ventral integument (figs. 2, 3, 9, 10) composed of fine spirochete-like wrinkles or ridges in uneven rows radiating between discs from center to periphery; mammillae absent. *Lateral structure*, *discs*, and *hairs*, essentially as in *A. r. reflexus*.

Capitulum (fig. 4) differing from that of *A. r. reflexus* as follows: *Basis capituli* typically with four small setae in each basolateral corner, and five small setae laterally on each side (in a very few specimens the number of setae is doubled; these setae, very small and difficult to discern,

[1]From Research Project NM 52 08 03.3, Bureau of Medicine and Surgery, Navy Department, Washington 25, D.C. The opinions and assertions contained herein are the private ones of the authors and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large. Accepted for publication March 22, 1960.

[2]Head, Department of Medical Zoology, United States Naval Medical Research Unit Number Three, Cairo, Egypt, U.A.R.

[3]Sanitarian Director, United States Public Health Service, Rocky Mountain Laboratory, Hamilton, Montana.

are frequently broken). *Hypostome* with bluntly rounded (seldom indented) apex bearing mere trace of corona or no corona; denticles of apical half of shaft 2/2, broad, short, and comparatively tapered, in three to five rows; hooklets of basal half 2/2 to 5/5 in approximately seven rows, less than half the size of apical denticles, also broad and blunt. *Palpi* with segments 1, 2, and 4 of subequal length, 3 approximately half the length of other segments; a single small seta arising ventrally from each palpal segment.

Eyes, spiracular plates, genital aperture, ventral "paired organ", and *folds*, as mentioned for *A. r. reflexus*. *Anus* situated slightly posterior of apical level of trochanter IV.

Legs arising from anterior two-fifths of body, apex of coxa IV anterior of midlength of body. Tarsi (fig. 5) with a very slight dorsal subapical protuberance or with none; apical margin blunt or tapered (not retrograde); tarsi with setae visible from lateral view on each leg, from I to IV, typically as follows: apicodorsal, 1, 1, 1, 1; subdorsal 4, 2, 2, 2; median 3, 3, 3, 3; apicoventral 4, 4, 4, 4; subventral 7, 5, 4, 5. Tarsal setae shorter and finer than in *A. r. reflexus*. *Claws* often appearing to be slightly more curved than in *A. r. reflexus*.

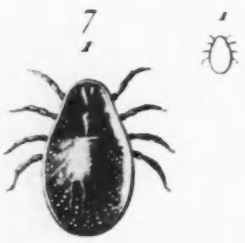


FIG. 1.—*Argas hermanni*, original illustration (Savigny 1826, plate IV, fig. 7).

MALE (figs. 6–8):—Similar to female except for slight secondary sexual characteristics. Measures from 3.4 mm. to 6.0 mm. in length and from 2.3 mm. to 3.8 mm. in width; average specimen 5.4 mm. long and 3.2 mm. wide. Genital aperture semicircular. Dentition as in female, denticles somewhat more blunt. Tarsi with lateral setae as in female except for an additional one subdorsally on 1 and 3 rather than 5 subventrally on II. Other characters essentially as in female.

NYMPH (figs. 11–21):—*Late instar nymphs* (figs. 11, 12, 15, 16, 20, 21), similar to adults in most characters; may equal adults in size. Integument as in adults except that lateral striations are very slightly wider. Genital aperture absent though a closed depression lies in its place. Capitular features as in adults except for size and number of setae ventrally on basis capituli; there are two in each basolateral corner, one laterally on each side, and one sublaterally on each side. Tarsi with subapical dorsal protuberances absent or slight; setae visible from lateral view on each tarsus, from I to IV, typically as follows: apicodorsal 1, 1, 1, 1; subdorsal 4, 1, 1, 2; median 2, 2, 2, 2; apicoventral 4, 4, 4, 4; subventral 4, 3, 3, 3.

First instar nymphs (reared, unengorged; figs. 13, 14, 17–19) closely resemble later stage nymphs except for smaller size, finer integumental elevations, which consist of short, irregular ridges and small points, and a few other details noted below. Measuring approximately 2.1 mm. in length and 1.1 mm. in width. Capitulum (figs. 17, 18) like that of larger nymphs except for slightly larger corona and shorter posthypostomal bristles, which do not reach level of midlength of palpal segment 2; basis capituli ventrally lacking setae except for a small basal pair; palpal segment 1 appearing to lack ventral setae, segments 2 to 4 each with a single ventral seta. Tarsi lacking any trace of a subapical dorsal protuberance, more gradually tapered distally than in adults and other nymphal instars; setae visible from lateral view on each tarsus, from I to IV, typically as follows: apicodorsal 1, 1, 1, 1; subdorsal 5, 1, 1, 1; median 1, 1, 1, 2; apicoventral 3, 3, 3, 3; subventral 4, 2, 2, 3.

LARVA (figs. 22–23), reared from Egypt and French West Africa, unengorged.—Body circular, measuring approximately 0.42 mm. in diameter. Capitulum anterior. A subcircular squamous area present on dorsal integument.

Setae of body and legs slightly less conspicuously fringed than those of *A. r. reflexus*; numbers differing from those of subspecies *reflexus* as follows: seven anterolateral pairs and eight posterolateral pairs (total of 15 pairs of dorsolateral hairs), seven setae on each posterior quadrant, and one seta on coxa I (coxae II and III each bear one moderately long and one minute seta); other setae equalling those of subspecies *reflexus* in numbers.

Capitulum: Basis capituli with slightly convex margins and rounded junctures; with two pairs of minute bristles on ventral surface. *Palpi* essentially as in *A. r. reflexus*. *Hypostome* elongate, lateral margins very slightly convex, apex gradually to bluntly rounded, a fine corona present; denticles moderate in size, elongate, narrow, pointed apically; dentition typically 3/3 inner file of five denticles extending from corona to midlength of shaft; the 10 denticles of median file gradually decreasing in size from apex to base; outer file of largest, laterally directed denticles numbering 9 to 11, gradually decreasing

in size from apex to base; denticles rarely forming 2¼/2¼, 2½/2½, or 3½/3½ files.

Legs long and stout, approximately 1.6 times as long as diameter of body, claws fairly long; pads (pulvilli) reduced; setae as illustrated.

MATERIAL EXAMINED

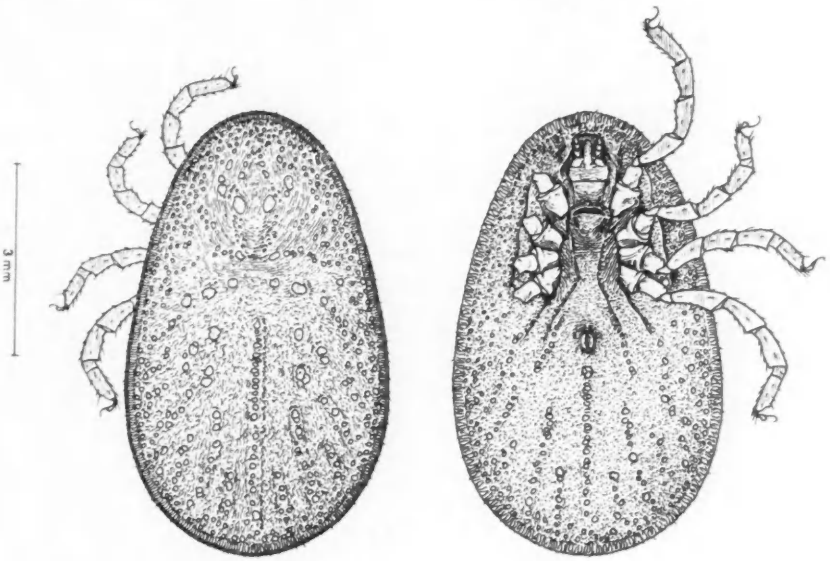
(with notes on hosts and habitats)

From domestic fowls (Egypt).—From pigeon houses in Cairo Governorate and Giza, Beheira, and Kafr El Sheikh Provinces, numerous localities and dates between 1950 and 1958 (about 2,000 individuals, all stages. See figures 24 and 25.

Domestic chicken, El Dakka, El Dirr, Aswan, 16 March 1956, 1♀.

Giza Pyramids, chambers beside: about 50 nymphs and adults, 18 June 1951; 2♂, 6♀, 12 May 1952.

Abu Rawash Pyramid and desert cliffsides within 1 mile of village: 9♂, 4♀, 9 nymphs, 13 May 1951; 17♂, 9♀, 37 nymphs, 12 June 1951; 3♂, 1♀, 13 June 1951; 2♂, 3♀, 4 nymphs, 8 August 1951; 1♂, 3♀, 2 nymphs, 18 September 1951; 1♂, 1 nymph, 29 October 1951; 3♂, 1♀ 10 December 1951; 8♂, 6♀, 8 nymphs, 8, January 1952; 2♂ ,1♀, 3 nymphs, 9 January 1952; 4♂, 12♀, 12 January 1952; 11♂, 3♀, 6 nymphs, 6 February 1952; 8♂, 12♀, 2 nymphs, 17 March 1952; 2♂, 10♀, 2 nymphs, 21 March 1952; 17♂, 8♀, 5 nymphs, 24 March 1952; 5♂, 7♀, 1 nymph, 2 June 1952; 1♂, 4♀, 4 nymphs,



2 3

Argas reflexus hermanni, female, from pigeon lofts, lower Egypt.
FIG. 2.—Dorsal view. FIG. 3.—Ventral view.

From wild birds (Egypt).—From Little Owls (North African form), *Athene noctua glaux* (Savigny, 1810). Most of our *Argas* specimens from wild birds originate from the Little Owl, which rests in holes in walls, crevices in antiquities, among piled stones, in old gasoline drums filled with stones, in trees, in cliffsides, in sandpiles, or in canal banks. The following material has been obtained from their nests or resting sites:

Karanis Greco-Roman ruins, Kom O Shim. Faiyum: about 50, all stages, January 1952, 8♂, 13♀, 6 nymphs, 29 May 1952; 5♂, 8♀, 14 nymphs, 20 larvae, 28 December 1953.

Sakkara Ruins, Giza: 15♂, 12♀, 34 nymphs, 31 May 1951; 3♂, 2♀, 6 February 1952.

22 September 1952; 14♂, 8♀, 6 nymphs, 9 November 1953; 5♂, 5♀, 22 June 1959.

From four nestling Lanner Falcons (Nubian form), *Falco biarmicus tanypterus* Schlegel, 1844: Abu Rawash, Imbaba, Giza, May 1957 (about 100 nymphs and adults reared from larvae); numerous others from same nest (fig. 26) in May 1958 and May 1959.

From a Long-legged Buzzard (North African form), *Buteo ferox cirtensis* Levaill., 1850: Cairo, 1954, 1 nymph.

From a nestling Hooded Crow (Mediterranean race), *Corvus corone sardonius* Kleinschmidt, 1903: Faiyum Province, 13 April 1952 (2 adults and 6 nymphs reared from larvae, and 16 larvae).

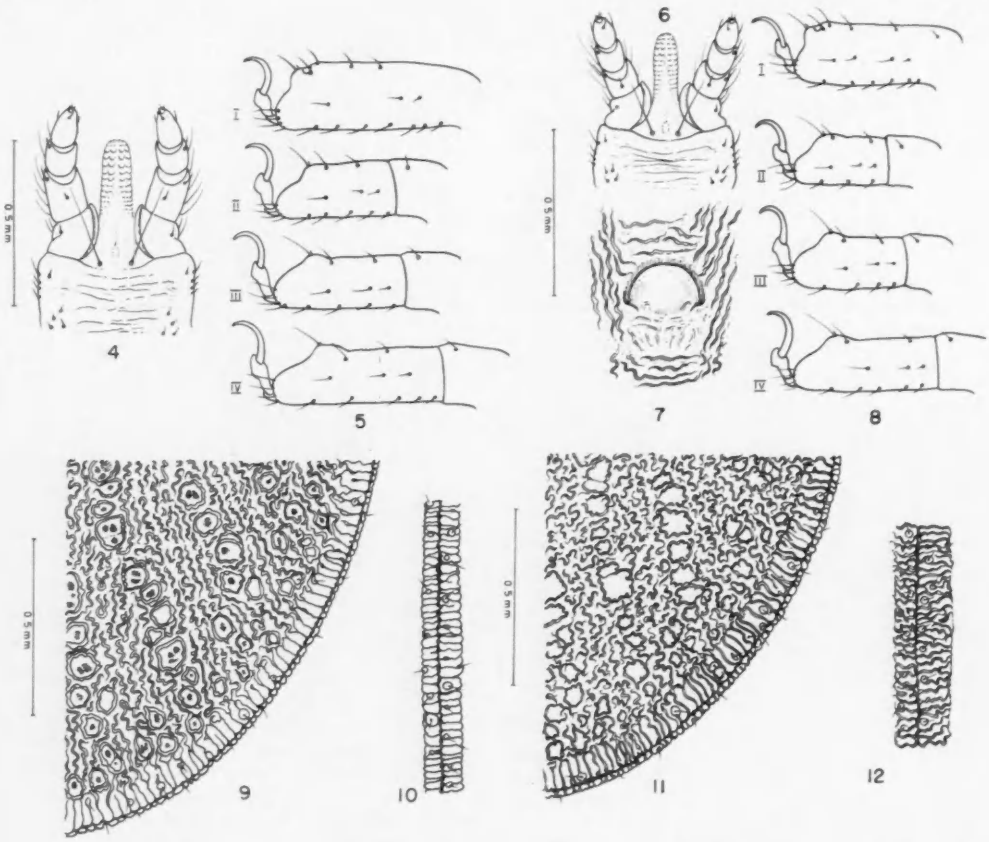
From *Corvus corone sardonius*: Kafr Mit Abu Ghalib, Shirbin, Gharabiya, 7 August 1953 (1 larva).

From crevices in desert cliff beside nest of Brown-necked Raven, *Corvus corax ruficollis* Lesson, 1831: near Kilometer 52, Cairo-Alexandria Road, Western Desert, 30 July 1959 (11♂, 6♀, 14 nymphs; about 100° F_1 progeny reared in laboratory).

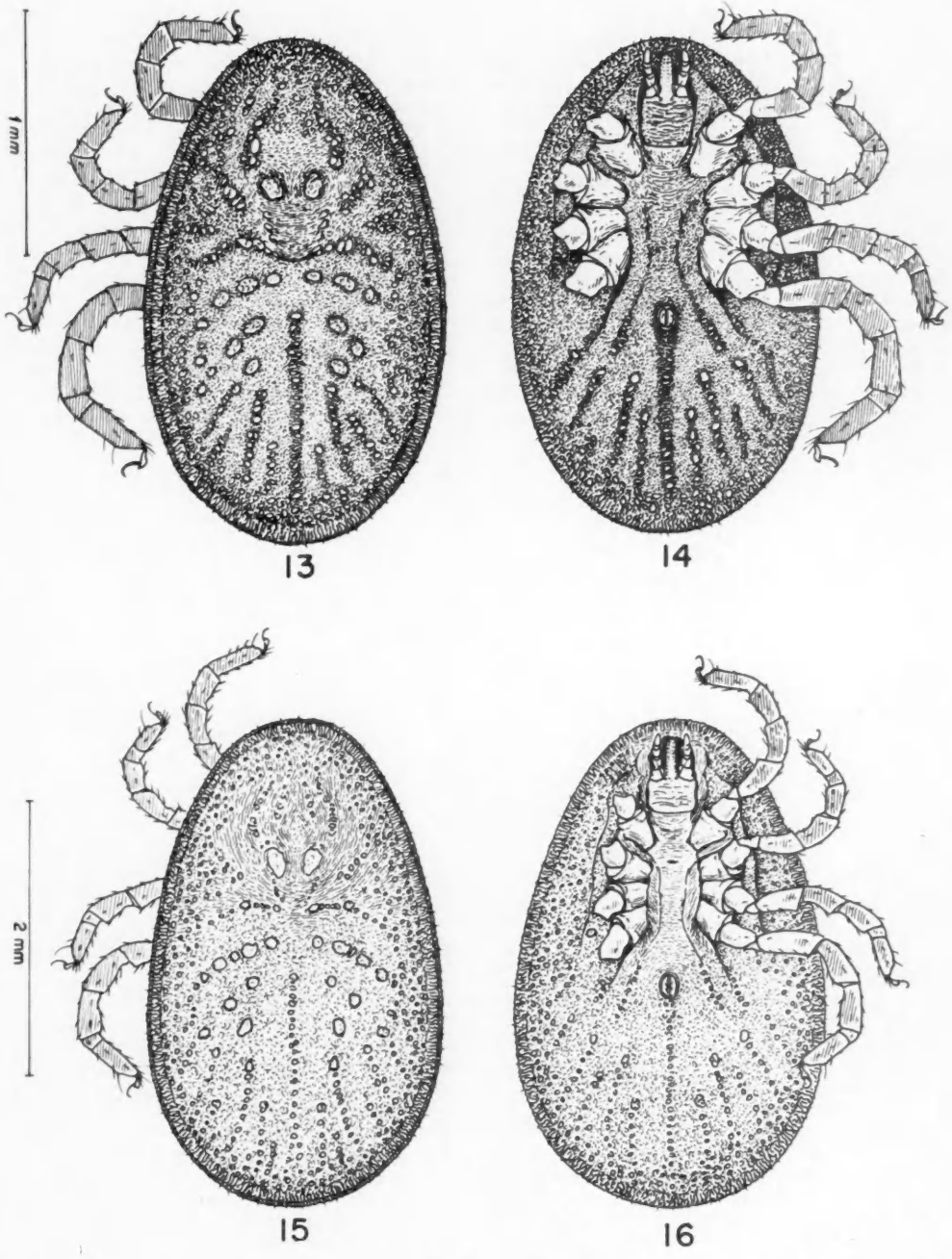
From migrating birds (*Egypt*).—Blue-throat (white-spotted form), *Luscinia svecica cyanecula* (Wolf, 1810) (rearing host No. 534): Abu Rawash, Imbaba, Giza, 16 March 1958 (numerous progeny being reared from nine larvae). This species, an uncommon winter resident in Egypt, winters elsewhere in North Africa as far south as Port Sudan. It breeds in Spain, France, and Central Europe to Russia. The *Argas* infestation may have been acquired anywhere between northern Sudan and Giza Province, Egypt.

From Blue Thrush or Rock Thrush (HH 4902), *Monticola saxatilis* (Linnaeus): Abu Rawash, Imbaba, Giza, 29 March 1959, 1 larva (rearing host No. 1334) [larva dropped from host 2 April; molted 13 April; nymph fed on pigeon 22 May; nymph molted to male on 19 June. Note single nymphal stage]. This migrant bird was trapped during its spring passage from tropical Africa, probably en route to European Russia or western Siberia. For further details on ticks and migration of this host species, see Hoogstraal and Kaiser (1958). The infestation appears probably to have been locally acquired.

From hedgehog burrow (*Egypt*).—Burrow of Egyptian Long-eared Hedgehog, *Hemiechinus auritus aegyptius* E. Geoffroy St. Hilaire, 1803: in desert 20 yards from cultivation, Abu Rawash, Imbaba, Giza, 22 May 1952, 18♂, 9♀, 29 nymphs (actual host unknown; see *Host Relationships*, below).



Argas reflexus hermanni from pigeon lofts, lower Egypt. FIG. 4.—Capitulum of female, ventral view. FIG. 5.—Tarsi I–IV of female, lateral view. FIG. 6.—Capitulum of male, ventral view. FIG. 7.—Genital area of male. FIG. 8.—Tarsi I–IV of male, lateral view. FIG. 9.—Dorsal integument of female, posterior quadrant. FIG. 10.—Lateral integument of female. FIG. 11.—Dorsal integument of large nymph, posterior quadrant. FIG. 12.—Lateral integument of large nymph.



Argas reflexus hermanni from pigeon lofts, lower Egypt. FIG. 13.—First-instar nymph, dorsal view. FIG. 14.—Same, ventral view. FIG. 15.—Late-instar nymph, dorsal view. FIG. 16.—Same, ventral view.

From other African areas.—From clothing of African woman, Kajiado, Kenya, December 1952, Dr. J. C. Likimani. This single female, reported by Heisch (1954) as *A. reflexus*, was kindly loaned to us by Dr. Heisch. The capitulum, which had been mounted separately, was not available. From the published illustration of this capitulum, it appears that a separate species may be involved, but distortion due to drying may account for the apparent differences. All features of the body and legs of this specimen are characteristic of *A. hermanni*.

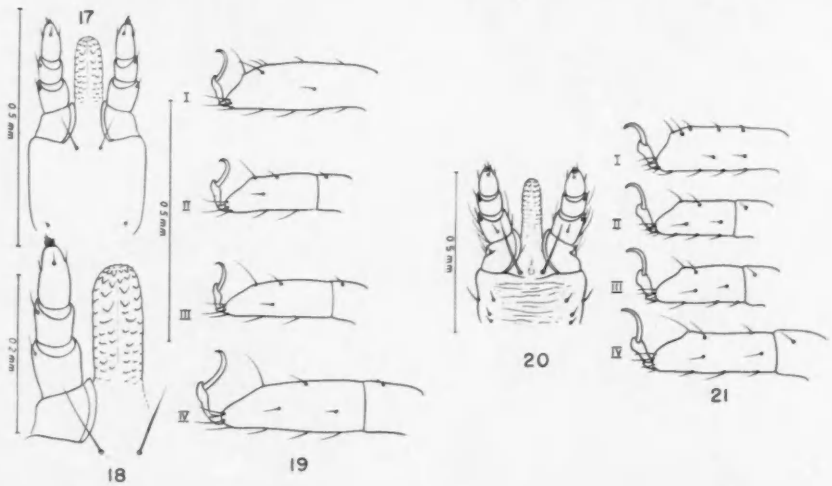
Domestic pigeon cote, Juba, Equatoria, Sudan Republic [2 nymphs, 1♂, 1♀, November 1949; 1 nymph, January 1950. See Hoogstraal (1956)].

A specimen, without further data, from the Neumann collection, identified by him as *A. hermanni*, was examined through the courtesy of Dr. P. C. Morel. It agrees with Egyptian specimens in all details. [Neumann (1911) listed this species from Egypt and Ethiopia.]

Correspondents at French institutions with classical tick collections inform us that no type material of *A. hermanni* exists today. A NEOTYPE is therefore selected and deposited in the United States National Museum. This is a female from a pigeonhouse, Abbassia, Cairo, Egypt, 14 June 1950, H. Hoogstraal. Specimens from the same lot are deposited in the major tick collections of the world, and others will be sent to interested persons upon request.

VARIATION

In the description of the female of *A. r. reflexus* (Hoogstraal and Kohls 1960) it was noted that different impressions of the type of integumental elevations are obtained from study of individual ticks preserved at different stages of engorgement or at different digestive periods. Such differences appear to be less confusing in adults of *A. r. hermanni*, where integumental elevations are finer and more regular. In nymphs of this



Argas reflexus hermanni from pigeon lofts, lower Egypt. FIG. 17.—Capitulum of first-instar nymph, ventral view. FIG. 18.—Hypostome and palpus, enlarged, of first-instar nymph, ventral view. FIG. 19—Tarsi I–IV of first-instar nymph, lateral view. FIG. 20.—Capitulum of late-instar nymph, ventral view. FIG. 21.—Tarsi I–IV of late-instar nymph, lateral view.

Chickenhouse, Kouroussa, Guinea, French West Africa, 1958; living and preserved material sent 1958 and 1959 by Dr. P. C. Morel (numerous specimens; all stages).

NEOTYPE

Argas hermanni was originally illustrated by Savigny (1826, plate IV, figure 7) (reproduced herein in fig. 1) and described by Audouin (1827, page 184), from Egyptian collections, as follows:

IX. 7. *ARGAS HERMANNI, Argas* d'Hermann.

On ne connaissait jusque dans ces dernier temps qu'une seule espèce d'argas, l'Argas bordé, *Argas reflexus*: celle qui est figurée ici lui ressemble quant á la forme de son corps. 7. 1. Individu très-grossi, vu en dessus. i, grandeur naturelle.

form that have dried before being placed in preservative, or which are preserved immediately after molting or when greatly engorged, the form of integumental elevations may appear to be quite variable.

In a small proportion of adults (less than 5%) examined from Egyptian wild-bird nests and pigeon houses, the tarsal protuberances are somewhat more elevated than is typical of the subspecies *hermanni* and in this respect approach those of the subspecies *reflexus* of Europe.

Specimens of *A. r. hermanni* from wild birds and their nests are mostly smaller in size than those from pigeon houses and often are somewhat wider in body outline than inhabitants of pigeon

houses. However, most pigeon-house populations contain a small proportion of specimens similar to those from wild birds, and a few specimens in several lots from wild birds are similar to those from pigeon houses in both body outline and large size.

With the assistance of Mr. Makram N. Kaiser, the dentition, chaetotaxy, and numerous other details of both sexes and all stages of numerous samples from pigeon houses and wild birds in Egypt have been examined with the aid of the stereoscopic and phase contrast microscope. No significant or insignificant differences, except generally for comparative size, could be discerned between samples from these two different sources. Remarks on these habitats are presented below.

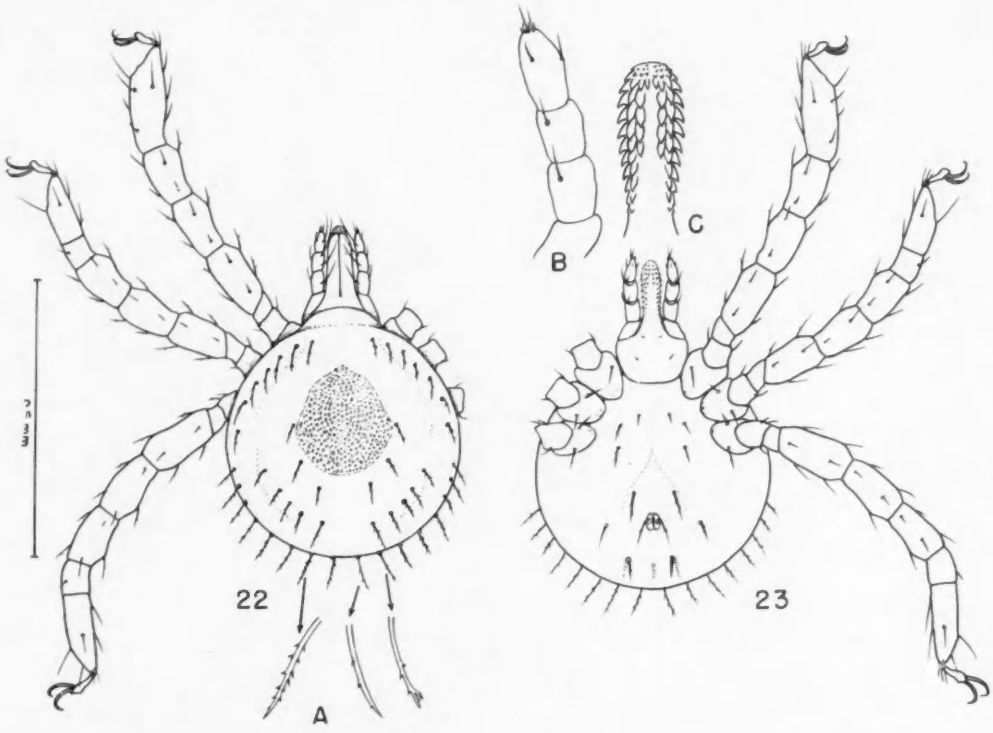


FIG. 22.—Unengorged larva, dorsal view. FIG. 23.—Same, ventral view. A, posterolateral setae, enlarged. B, palpus, enlarged. C, hypostome, enlarged.

RELATED FORMS

Adults of the subspecies *hermanni* are distinguished from those of *reflexus* chiefly by their generally smaller size; broader, and more bluntly rounded hypostomal denticles; and smaller tarsal subapical dorsal protuberances which are blunt rather than retrograde distally. Other critical adult characters, chaetotaxy, formation of integumental elevations, etc., exist but may be more difficult to discern.

Nymphs of both subspecies also differ in form of hypostomal denticles, those of *hermanni* being broad and blunt and those of *reflexus* narrow and sharp. The first-instar nymph of *hermanni* lacks subapical dorsal protuberances on the tarsi; these are usually slightly developed in first-instar nymphs of *reflexus* and more so in later instars. Posthypostomal bristles in *hermanni* nymphs are slightly more than half the length of those in *reflexus* nymphs. Other differentiating characters are found in details of chaetotaxy, integumental elevations, etc.

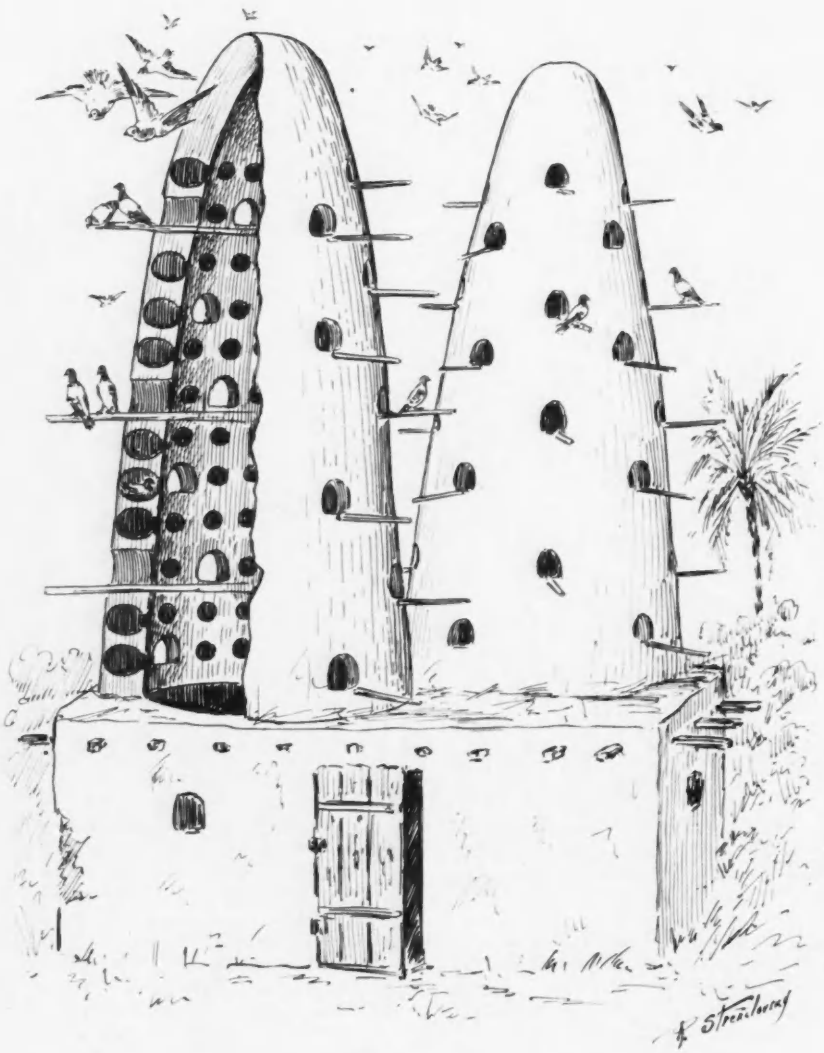
Larval dentition of *hermanni* is typically 3/3, that of *reflexus* 2/2. The number of dorsal setae of *hermanni* are: anterolaterals 14 (vs. 30), posterolaterals 16 (vs. 24), on posterior quadrant 7 (vs. 9). Fringing of *hermanni* setae is less conspicuous than that of *reflexus* setae. The squamous area of *hermanni* is wide, almost subcircular, while that of *reflexus* is narrowly elongate.

Argas cooleyi Kohls and Hoogstraal (1960) of western North America, is more like the subspecies *reflexus* than *hermanni* in most respects.

Larval differences are especially distinct; dorsal setae in *cooleyi* number 16 anterolaterals, 28 posterolaterals, and 9 on each posterior quadrant (in *reflexus*, these are 30, 24, and 9). Setal fringing in *cooleyi* larvae is much lighter than in either subspecies of *reflexus*. Larval dentition of *cooleyi* is 2/2 as in *A. r. reflexus* but the number of denticles is much fewer, the size is much larger, and the hypostome is stouter and shorter. The dorsal squamous area of *cooleyi* is subcircular, thus rather similar to that of *hermanni*, but quite different from that of *reflexus*.

Adult integumental elevations of *cooleyi* differ somewhat from those of both *reflexus* subspecies, as do the lateral flange elevations. Adult tarsal dorsal subapical protuberances are only slightly elevated but are more retrograde distally than those of the subspecies *reflexus*. Other differences are found in chaetotaxy, dentition, etc.

A. (*A.*) *persicus*, one of the most widely distributed ticks in the world, on occasion infests wild birds, especially those that build large nests of sticks in buildings or trees. The larvae of this and other argasids are often difficult to iden-



24

FIG. 24.—Sketch of typical Egyptian pigeon house, to show construction.

tify when taken from wild hosts, owing to damage during removal, normal wear, and degree of distention with blood. Althouth *A. persicus* falls in the subgenus *Argas*, it is not a member of the *reflexus* group. However, its close relation to this group is shown by similarity of larval stages. Persons working in areas where both *persicus* and *hermanni* larvae may be encountered on birds might easily have trouble in differentiating these two forms. Adequate descriptions and illustrations of *persicus* larvae are not generally available in literature. Therefore, for both academic and practical interest, a description of the larva of *A. persicus* (as reared from adults infesting domestic chickens in the Cairo area) is presented below, together with a list of differences by which *persicus* and *reflexus* group larvae may be differentiated.

A. persicus (*larva*, unengorged, figs. 27–28). Body subcircular, wider posteriorly, anterior margin almost truncate; measuring approximately 0.70 mm. in length and in width. A comparatively small, circular squamous area present on dorsal integument.

Setae of body with very slight fringing (visible only under oil-immersion magnification) mostly confined to apex of setae. Setae of legs and capitulum with very fine lateral fringes. Setae of dorsal surface of body numbering 5 anterolateral pairs and 10 posterolateral pairs (total of

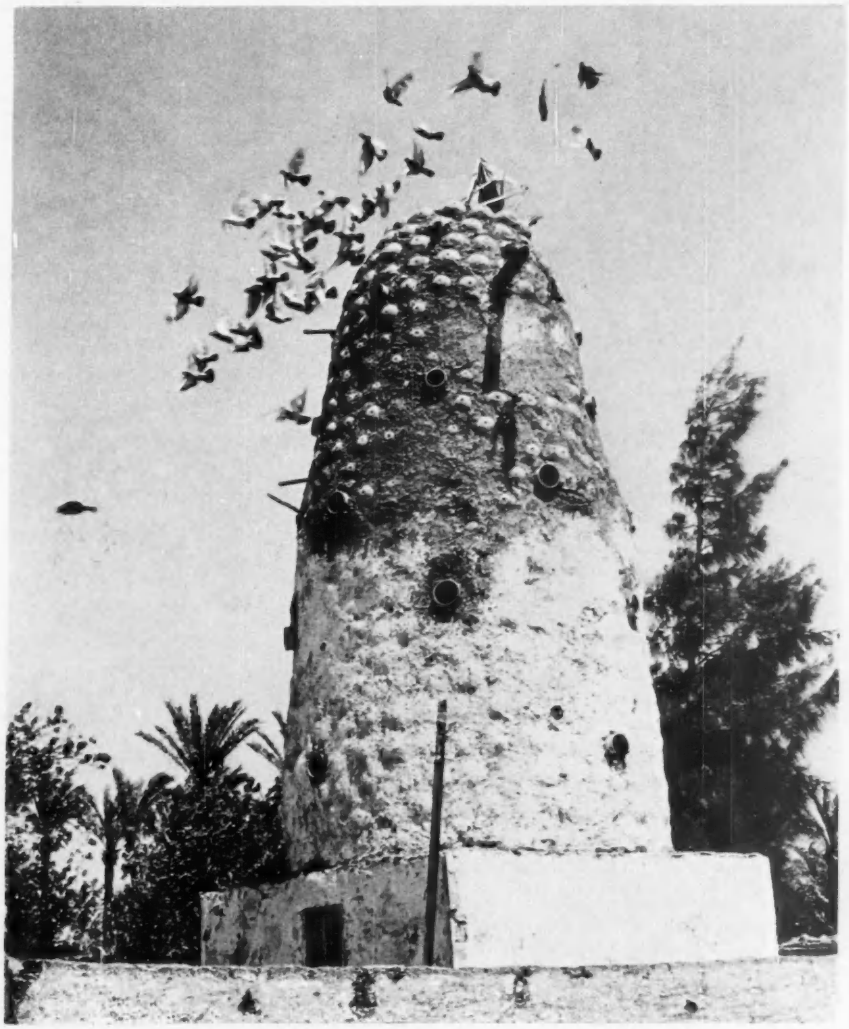


FIG. 25.—Exterior of typical Egyptian village pigeon house infested by "domestic" *A. r. hermanni* demes.

15 pairs of dorsolateral setae), 3 pairs bordering squamous area, 3 anterior submedian pairs, and 7 setae on each posterior quadrant. Ventral setae of body numbering three pairs in intercoxal area, two setae on each coxa, one seta from each valve of anus, and three circumanal pairs.

Basis capituli with two pairs of short bristles on ventral surface. *Palpi* with a single sublateral seta ventrally on each side of segments 2 to 4; no setae on segment 1; several setae on each segment dorsally; segment 4 twice as long as 3; segments 1 to 3 subequal in length. *Hypostome* elongate, lateral margins parallel or slightly diverging, apex gradually to bluntly rounded (may be very slightly indented); corona moderate, consisting of three or four rows of small hooklets. Denticles comparatively large, widely elongate, tapered to fairly sharp apex; dentition typically 2/2 in files of seven and six extending full length of shaft; dentition occasionally 2½/2½, with an inner file of one to three denticles.

From the subspecies *reflexus*, *persicus* larvae may be distinguished by their more elongate apical palpal segment, larger and fewer hypstomal denticles, smaller and circular squamous area, much lighter fringing of body setae, and the considerable difference in number and placement of dorsal body setae. The presence of anterior submedian setae and of three rather than one pair of setae bordering the squamous area in *persicus* larvae appears to be as distinct a criterion for separating the *persicus* group (i.e. *A. persicus*) from the *reflexus* group as is the presence of "cells" or "ridges" on the lateral integument of adults of these two groups. In addition, it may be noted that postpalpal bristles are present in adults and nymphs of *persicus* but are lacking in species of the *reflexus* group.

The same characteristics differentiate *persicus* and *hermanni* larvae. In *hermanni* larvae, in which setal fringing is comparatively slight, differences in this character may be more difficult to discern. The terminal palpal segment of *hermanni*, longer than that of *reflexus*, approaches but does not equal that of *persicus* in length. The dentition of *hermanni* is typically 3/3, that of *persicus* 2/2, but the hypostome is frequently broken in specimens removed alive from the host.

FIG. 26.—Barren desert cliff with nest of *Falco biarmicus tanypterus*, infested by "feral" *A. r. hermanni* demes.

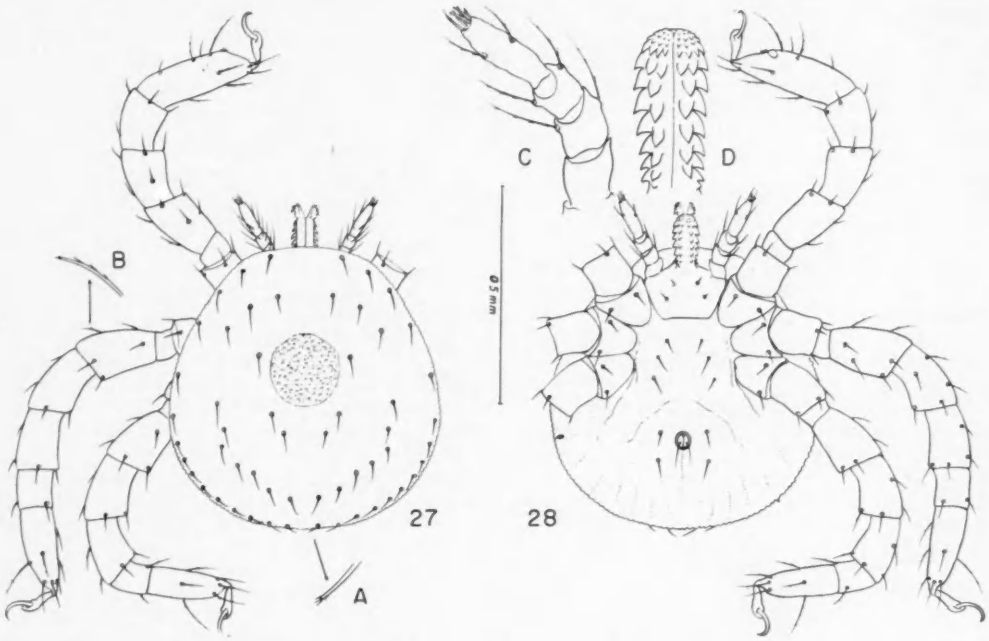
DISTRIBUTION

A. r. hermanni is widely established in Egyptian cultivated and desert areas as well as in savannahs of French West Africa (Guinée, Côte d'Ivoire, Haute Volta, and Dahomey). Small numbers of specimens are known from Equatoria Province, Sudan Republic, and from Kajiado, Kenya, and have been reported by Neumann (1911) from Ethiopia; whether this material derives from established populations or from adventitious introductions on migrating wild birds or imported domestic birds remains to be ascertained.

The French West African localities noted above are in tropical grasslands (Sudanese Savannah District), with 10 or 20 or more times the annual rainfall of Egypt and a more restricted range of temperatures than Egypt.

HOST RELATIONSHIPS

In Egypt, "domestic" demes of *A.* (*A.*) ***reflexus hermanni*** are common in domestic pigeon houses (figs. 24, 25) and "feral" demes commonly infest Little Owls, *Athene noctua glaux* (Savigny, 1810) as well as Lanner Falcons, *Falco biarmicus tanypterus* Schlegel, 1844, Hooded Crows, *Corvus corone sardonius* Kleinschmidt, 1903, and Brown-necked Ravens, *Corvus corax ruficollis* Lesson, 1831. Migrating birds taken in Egypt appear to have acquired their infestation here or in northern Sudan; these are a Bluethroat, *Luscinia svecica cyanecula* (Wolf, 1810) and Blue (or Rock) Thrush, *Monticola saxatilis* (Linnaeus, 1766). Only a single specimen has been taken on a domestic chicken in Egypt, though more intensive examination of these birds may reveal a higher



Argas persicus, reared from chickens in Cairo area, Egypt. FIG. 27.—Larva, unengorged, dorsal view. FIG. 28.—Same, ventral view. A, posterolateral seta, enlarged. B, leg seta, enlarged. C, palpus, enlarged. D, hypostome, enlarged. One pair of circumanal setae lacking on specimen illustrated.

We postulate that larvae of African *A. r. hermanni* and of European *A. r. reflexus* are rather frequently carried into the other's continental range on migrating birds. We have no evidence, however, that either of these forms has become established outside of its normal geographic range. In order to know the possible effect of interbreeding in nature we are now attempting to cross *A. r. hermanni* and *A. r. reflexus* in the NAMRU–3 laboratories.

incidence of infestation. In West Africa, however, Dr. P. C. Morel (personal correspondence) commonly finds *A. r. hermanni* in chicken houses [Guinée (Kouroussa), Côte d'Ivoire (Korhogo), Haute Volta (Gaoua and Boroum-Boroum), and Dahomey (Bessassi)]. The specimens from Korhogo were taken together with others of *A.* (*A.*) *persicus*.

During the past several years literally thousands of specimens of *A.* (*A.*) *persicus* from a

number of rookeries of the Cattle Heron, *Bubulcus i. ibis*, in the Cairo area have been examined (Hoogstraal 1956, pp. 62-63). Notably, *A. r. hermanni* has not been found in these situations. *A.* (*A.*) *persicus* has also been taken in Egypt on wild doves, crows, and ravens, and in their nests, but never on the same hosts or in the same nests in which *A. r. hermanni* occurs.

The exceptional finding of *A. r. hermanni* in a hedgehog burrow in Egypt may result from the temporary utilization of this shelter by an owl, *Athene noctua glaux*, which rests in almost any small crevice in or near the ground.

The frequent finding of American *A.* (*A.*) *cooleyi* Kohls and Hoogstraal (1960), in and near cliff swallow nests and the single available European specimen of *A. r. reflexus* from a Crag Martin suggests the possibility that birds of the family Hirundinidae may have been the primitive hosts of this group of ticks. In Australia, the Fairy Martin or Bottle-nest Swallow, *Hylochelidon ariel* Gould, is the host of *A. lagenoplastis* Froggatt, another member of the *reflexus* group. We have not found *hermanni* on swallows or martins or in their nests in Egypt but, unfortunately, rather few of these birds or situations have thus far been examined.

From presently available data, it appears that *hermanni* and possibly other *reflexus* group forms may be adaptable to parasitizing a variety of birds but that survival is more closely associated with the degree of protection from environmental conditions offered by the host's nests or by environmental situations immediately adjacent to these nests. Swallows and martins nest in mud structures often on cliffsides or in caves near water, or on the sides of buildings or undersides of bridges. Nearby crevices usually offer some retreat for the ticks during postfeeding and prefeeding periods. Domestic pigeons are usually maintained in equally protected and creviced man-made structures. If the nest environment is an important factor in survival, it would appear that retreats of the Little Owl in Egypt are often quite suitable for *hermanni* survival. More exposed nests of other birds, falcons, buzzards, crows, and ravens, probably satisfy the minimum environmental demands of this form in Egypt. Owing to the wide geographic, ecological, and environmental range of habitats in which *hermanni* populations exist and/or thrive, it may be very difficult ever to specify a set of survival factors for all populations of this tick or to define exact environmental and host relationships.

DISEASE RELATIONSHIPS

In Egypt, several viruses, in two or more new groups, have been isolated from *A. r. hermanni* and *A. persicus*, and one of these was also isolated from children with acute febrile illness. A strain of West Nile virus (No. 1140) was isolated from *hermanni* ticks taken from a pigeon house at Esbet Chenuda on 8 January 1954 (R. M. Taylor, personal correspondence). West Nile virus also infects pigeons on this farm. The winter infection of these ticks, at a season when the human disease is not apparent, suggests a possible overwintering host of West Nile virus.

DISCUSSION

Thriving demes of *A. r. hermanni* exist in Egypt under extremely dissimilar ecological conditions. Biologically, it is difficult to believe that a single subspecies is so widely adaptable. Morphologically, superficial differences in appearance between individuals from sheltered domestic pigeon cotes and from exposed wild bird nests in desert cliffsides also suggest different taxonomic forms. Comparative study of large samples reveals no specific or subspecific diversity. Qualitatively, the range of morphological variation is the same in both samples. Quantitatively, most individuals from domestic situations are uniform in appearance while many from wild habitats are, on casual examination, quite variable. In other parts of Africa, as mentioned below, populations of *A. r. hermanni* inhabit other ecological zones and infest domestic chickens as well as pigeons.

In Egypt, raven- and falcon-parasitizing *hermanni* ticks live under desert conditions as extreme as any in the world. They feed on nestling and parent birds in hot, dry, exposed nests of weathered sticks (fig. 26) for 2 to 3 months each year, then retreat into nearby rock crevices where they remain, without food, till the next nesting season 9 or 10 months later. Those infesting Little Owls live under much more variable microclimatic conditions though their hosts are usually more or less constantly available throughout the year. Little Owls rest and nest in desert cliffsides as climatically rigorous as those in which ravens and falcons breed, but also utilize cooler, shaded, and somewhat more humid spaces among rocks on the ground, in walls, in trees, or in canal banks.

Parasites in domestic pigeon houses are provided with an ample source of nourishment the year around. Hundreds of birds live and tend their young in clay pots lining the thick mud walls of these structures (figs. 24, 25) and thousands of ticks find shelter in cracks within a few inches of their hosts. The interior of these buildings is constantly dark and comparatively cool and humid. Pigeon houses such as those illustrated, common throughout the cultivated areas of Egypt, provide both human food and fertilizer for fields. Infestation of these houses by *hermanni* ticks is quite erratic, for reasons that we do not yet know.

Samples of *hermanni* from pigeon houses consist of mostly large, uniform ticks, among which only a few are small or differently shaped. Those from wild-bird nests vary greatly in size, outline, color, prominence of tarsal protuberances, stret-

ching between integumental elevations and other features; their maximum size is rarely larger than the average of those from domestic pigeons but very large individuals occur in both situations.

It is of interest to observe the marked homogeneity of the *hermanni* deme on domestic pigeons and fowl in contrast with the heterogeneity of wild-bird parasites. This phenomenon would seem to be contrary to that found in most organisms, in which a high degree of adaptation to extremely demanding environmental condition is accompanied by a high degree of specialization and structural uniformity, a direct contrast to the situation observed in Egyptian *hermanni* populations.

ACKNOWLEDGMENTS

For furnishing unpublished data and living specimens of *A.* (*A.*) *reflexus hermanni* from French West Africa, and for comparing additional West African and Egyptian samples, we are especially grateful to Dr. P. C. Morel, of Dakar, who also sent us a Neumann-identified specimen of this form for study. Dr. R. Heisch, of Nairobi, kindly sent the only specimen of *hermanni* known from Kenya for comparison.

At NAMRU-3, Cairo, Mr. Sobhy Gaber reared the living material; Messrs. Makram N. Kaiser, Sobhy Gaber, Sayed Metwally, and Ezzat Guindy assisted in collecting specimens; and Mr. Roman Strekalovsky prepared illustrations.

REFERENCES CITED

Audouin, J. V. 1827. Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française, publié par les ordres de sa majesté l'empereur Napoléon le Grand. 2nd ed., **22**, Zool. Paris.

Heisch, R. B. 1954. First record of *Argas reflexus* (Fabricius) Latreille, 1796, from East Africa. East African Med. Jour. 31(3): 89–91.

Hoogstraal, H. 1956. African Ixodoidea. I. Ticks of the Sudan (with special reference to Equatoria Province and with preliminary reviews of the genera *Boophilus*, *Margaropus*, and *Hyalomma*). Washington, D. C.: Navy Department. 1,101 pp.

Hoogstraal, H., and **M. N. Kaiser.** 1958. Observations on Egyptian *Hyalomma* ticks (Ixodoidea, Ixodidae). 2. Parasitism of migrating birds by immature *H. rufipes* Koch. Ann. Ent. Soc. America 51(1): 12–16.

Hoogstraal, H., and **G. M. Kohls.** 1960. Observations on the subgenus *Argas* (Ixodoidea, Argasidae, *Argas*). 1. Study of *A. r. reflexus* (Fabricius, 1794), the European Bird Argasid. Ann. Ent. Soc. America 53(5): 611–18.

Kohls, G. M., and **H. Hoogstraal.** 1960. Observations on the subgenus *Argas* (Ixodoidea, Argasidae, *Argas*). 2. *A. cooleyi*, new species, from western North American birds. Ann. Ent. Soc. America 53(5): 625–31.

Neumann, L. G. 1911. Ixodidae. Das Tierreich 26. Berlin. 169 pp.

Savigny, J. 1826. Description de l'Égypte. Planches de Zoologie. Paris. 51 plates.

THE EUROPEAN CORN BORER, PYRAUSTA NUBILALIS, AND ITS PRINCIPAL HOST PLANT. VIII. LABORATORY EVALUATION OF HOST RESISTANCE TO LARVAL GROWTH AND SURVIVAL[1]

STANLEY D. BECK AND EDWARD E. SMISSMAN[2]
University of Wisconsin, Madison

ABSTRACT

Methods employed in the study of host plant resistance to the European corn borer are described and analyzed. Procedures for plant sampling, chemical fractionation, and bioassay are discussed. Laboratory rearing of the corn borer on purified dietary media is described in detail. Application of the experimental methods to investigations of plant resistance problems involving other insect and plant species is discussed.

The problem of evaluating varietal resistance to the European corn borer is one that requires more experimental information than can be obtained by any single technique. Field evaluations, phenological investigations, and genetic studies have all played a role in the development of borer-resistant lines of corn. Recent studies on the identity of physical and chemical factors involved in the borer's orientation and behavior on the corn plant (Beck 1956a, b), and on the chemical factors responsible for host plant resistance (Beck 1957a, b, Beck et al. 1957a, b, Loomis et al. 1957, and Smissman et al. 1957a, b) have opened the way for the effective application of laboratory techniques to problems involved in plant resistance.

It is not likely that laboratory estimation of resistance can be expected to replace field evaluation, for the final test of resistance must be measured in terms of what occurs in a field of corn. Field observations can measure resistance

[1]Approved for publication by the director of the Wisconsin Agricultural Experiment Station. This study was supported in part by a research grant from the National Institutes of Health of the U. S. Public Health Service. Accepted for publication May 5, 1960.

[2]Present address: Department of Pharmaceutical Chemistry, University of Kansas, Lawrence.

only in terms of one end point—borer infestation. The laboratory procedures that have been developed permit resolution of the complex of factors contributing to that end point.

Identification of insect and plant factors involved in host resistance requires separation of the insect from its host plant. Borer larvae on a corn plant are on an unstable medium, which, because of metabolic and growth patterns, is unsuitable as an experimental substrate. This problem is aggravated rather than solved through the use of excised plant tissues as media on which to test larval growth, behavior, and survival. On such dead or dying plants, the very conditions on which experimental information is sought are subject to unmeasured changes and cannot be assumed to be comparable to normal host plant conditions.

Separation of the borer from the corn plant requires the use of adequate rearing methods and a stable dietary medium that may be varied systematically under controlled conditions. Information on the nutritional requirements of the borer (Beck et al. 1949, Beck 1950, 1953) and an aseptic rearing technique (Beck and Stauffer 1950) have provided the means of meeting these requirements. Although these methods permit controlled experimental conditions, the situations under which the borers are placed are highly artificial compared to their natural environment. The use of *Penicillium chrysogenum* as a substitute for the European corn borer in bioassays of chemical resistance factors (Beck 1957, Beck and Stauffer 1957, Loomis et al. 1957) is also an artifice whose validity might be questioned. In order to use such laboratory methods in resistance studies, it is essential that the methodological limiting factors be identified and standardized, and that the assumption of comparability between laboratory results and field observations be carefully tested. This paper deals with these problems, and with the characteristics of host plant resistance as disclosed by application of the methods described.

METHODS

Plant Sampling.—Since the objective of the bioassay techniques described below is to obtain quantitative measurements of the effect of host plant constituents on the growth and survival of the borer, plant sampling is a highly critical procedure. It is of primary importance to sample plant parts that are at the site of attack by the borer at a particular stage of plant growth. There is little to be gained by sampling parts of the plant not directly involved in the establishment and feeding of the larvae. Thus, phenological aspects of both the plant and the insect must be considered, as well as the feeding behavior of the borer on the corn plant (Beck 1956a, 1957b).

Plant tissue samples should be collected at about the same time each day, so that different plants being studied will be in comparable metabolic states at the time tissue samples are taken. It is well known that dark metabolism in plants is quite different from their light metabolism, and Loomis et al. (1957) found that the resistance-factor content of corn seedlings held in the dark was but one-fourth that of seedlings exposed to light for 12 hours preceding analysis. This effect of light was confirmed by Virtanen et al. (1957). Presumably because of the effects of light intensity, corn plants grown under greenhouse conditions contain very low levels of resistance-factor activity, and varietal comparisons did not prove feasible under such conditions.

Plant-tissue samples were collected, weighed, and frozen with as little delay as possible. They were stored in a frozen state until extracted. Although relatively stable, resistance-factor activity was found to decline if the frozen samples were stored for longer than 8 months.

Preparation of Plant Tissue Extracts.—Aqueous concentrates of plant-tissue samples were used in bioassays of resistance-factor activity. Prior to extraction, the plant samples were dried at 40° C. in a low-pressure drying oven. The dried sample was then weighed and ground in a motor-driven mill. Two hundred grams of the dry, ground sample was extracted about 3 hours in 3 liters of boiling water. After filtering, the residue was discarded, and the filtrate was concentrated under reduced pressure until 1 milliliter represented 5 grams of the original fresh plant tissue. The pH of the concentrate was adjusted to 6.5. The concentrate was then autoclaved for 10 minutes at 17 pounds pressure, following which the pH was again adjusted to 6.5. This treatment resulted in the formation of a proteinaceous sludge, which was removed by centrifugation and discarded. We have never found resistance-factor activity in this precipitate. The volume of the concentrate was again adjusted so that 1 milliliter represented 5 grams of plant tissue. This type of preparation is referred to below as the *crude concentrate.*

The crude concentrate may also be fractionated in order to effect a separation of the different substances contributing to the total resistance-factor activity. The fractionation scheme used has involved extraction of the crude concentrate with an organic solvent. The crude concentrate was acidified (HCl) to pH 2, and extracted with five or more small volumes (20 ml.) of diethyl ether. The ether extracts were combined and evaporated to dryness under reduced pressure. The residue was taken up in water, adjusted to original volume, and brought to pH 6.5. This "ether-soluble fraction" contained Resistance Factor A (6-methoxybenzoxazolinone) and Resistance Factor C (Beck 1957). Separation of RFA from RFC is possible by chromatographic methods (Beck et al. 1957, LaPidus unpubl.), but for most assay purposes such a separation is unnecessary.

Although RFC has not yet been isolated in highly pure form, results to date show that its molecule includes RFA as a constituent. Its activity appears to be largely dependent on the RFA portion of the molecule. For this reason RFA and RFC may be treated as essentially identical.

The ether-extracted crude concentrate was boiled to remove traces of ether, adjusted to pH 6.5, cleared by centrifugation, and brought to volume. The "ether-insoluble fraction" contained Resistance Factor B (Beck 1957, Beck and Stauffer 1957). Other than its relative insolubility in ether from an acid solution, nothing is known of the properties of RFB.

The methods used in preparation of plant concentrates and assay media (see below) were such that any heat-labile or unstable resistance factors present in the plant samples would have been destroyed. This limitation of the techniques may not be serious in the study of plant resistance to the European corn borer, but might preclude the use of such methods in some insect-plant problems. Heat-labile toxic factors have been found to be important in host utilization in some instances (Ishii 1949, Lipke and Fraenkel 1955).

Chemical Analysis of 6-Methoxybenzoxazolinone.—A specific quantitative method for estimating plant-tissue concentrations of 6-methoxybenzoxazolinone was described in detail in an earlier publication (Beck et al. 1957). The technique involved extraction of small (1–2 g.) fresh or frozen samples of plant tissue with diethyl ether. The ether extracts were purified chromatographically with acid-washed aluminum oxide (Merck). The resistance factor was eluted from the column with an ether-ethyl alcohol solvent mixture. The concentration of the compound was then estimated spectrophotometrically by its extinction at 285 mμ. The absorption spectrum of 6-methoxybenzoxazolinone shows a pronounced peak in the ultraviolet at 285 mμ (Loomis et al. 1957).

The chemical method does not allow an estimation of RFC concentration, as extraction and purification does not result in hydrolysis of RFC to release the RFA constituent. Such release and subsequent determination of the RFA component may be effected through the use of an acid-alumina column. In this case, the plant extract should be moved very slowly on the column, so that the RFC is exposed to acid conditions for several hours during column development and elution. Such a procedure will hydrolyze RFC, and the 6-methoxybenzoxazolinone component in the column eluate may be estimated quantitatively as described above.

European Corn Borer Bioassay of Resistance Factors.—Resistance-factor activity contained in crude and purified plant concentrates was estimated by measuring their effects on the growth of newly hatched borer larvae. A purified rearing medium was used, and by standardizing the amounts of plant concentrates added to the diets, information was obtained on the relative resistance-factor content of samples of different plant species, varieties, ages, tissues, and growing conditions.

The aseptic rearing method of Beck and Stauffer (1950) was found to be adequate, although a few modifications were found to improve its efficiency and convenience. The dietary medium used in resistance assays differed from the basal diet employed in studies of normal growth and nutrition (table 1). The principal difference was in the dietary concentration of sugar (dextrose). The lower dextrose content of the resistance assay diet corresponds to the approximate sugar concentration found in growing foliage of the corn plant (Beck 1956a). It has been shown that the manifestation of resistance is partly dependent upon the sugar concentration of the dietary substrate (Beck 1957b). Brewers yeast powder was used in the resistance assay diets, replacing the vitamin mixture included in the basal diet. This substitution was a matter of convenience, as either vitamin source was nutritionally satisfactory. In regard to the remaining constituents, the two types of media were essentially identical.

Table 1.—Composition of purified diets used in studies of nutrition and host-plant relationships of the European corn borer.

Constituent	Dietary concentration (mg/g)	
	Basal diet	Resistance diet
Water	860.0	857.1
Bacto-agar	23.5	22.8
Fibrous cellulose	14.0	11.4
Dextrose	36.0	7.1
Casein (vitamin test)[a]	36.0	35.7
Corn oil (+1% alpha tocopherol)	1.5	1.5
Cholesterol[a]	1.5	2.7
Inorganic salts[b]	3.4	4.3
B vitamin mixture[c]	1.1	—
Brewers yeast powder[a]	—	28.5
Choline chloride	—	0.4
Leaf factor source[d]	23.0	28.5

[a]Nutritional Biochemicals Corp.
[b]Salts "W", Nutritional Biochemicals Corp.
[c]See table 2.
[d]Spray-dried alfalfa juice.

Plant concentrates were added to resistance assay media at the expense of the volume of water normally used. Two concentrations were usually assayed in varietal and plant age studies. The lower concentration involved the incorporation of 20 ml. of plant concentrate per 100 g. of medium. This resulted in the diet's being an

approximate gram-for-gram reconstitution of the original fresh plant sample. The higher assay level contained twice as much plant concentrate, each gram thereby being equivalent to about 2 grams of plant tissue. Assay media were prepared by mixing the ingredients in a boiling water bath by means of a power mixer. The media were then transferred to covered 90x50 mm. crystallizing dishes and sterilized by autoclaving for 20 minutes at 17 pounds per square inch. Using sterile glass cutting and transfer devices (Beck and Stauffer 1950), cylindrical pieces of the cooled and gelled diets were transferred to sterile, cotton-plugged shell vials (23x85 mm.) under aseptic conditions.

Aseptic rearing conditions necessitated surface sterilization of the borer eggs prior to hatching. This required that the egg masses be separated, so that all surfaces of the component eggs might be exposed to an antiseptic treatment. Borer egg masses in the "black head" stage of development were separated by trypsin digestion. A 2 percent solution of 1:300 commercial trypsin, buffered at pH 8.0 with 0.05M phosphate buffer, was used. Trypsin incubation at 35° C. with continuous or frequent agitation separated the eggs in about 45 minutes. Eggs were removed from the enzyme solution by means of a straight-tipped medicine dropper. When such a dropper is held vertically, the borer eggs settle to the tip, making it possible to transfer 50 or more eggs in a single drop of liquid. Using this technique, eggs were transferred through six rinses of distilled water and one rinse of 40 percent ethyl alcohol. They were then surface-sterilized by a 6-minute wash in 0.1 percent mercuric chloride and a 1-minute rinse in 70 percent ethyl alcohol. Groups of from 50 to 70 surface-sterilized eggs were transferred to sterile agar slants and incubated at 30° C. until hatching. The agar slants were made up in large (100 ml.) test tubes, and contained 2 percent agar without nutrients. All of the viable eggs hatched within 18 hours, at which time the larvae were transferred to individual rearing vials containing dietary media. Larval transfer was effected by means of a sterile nichrome wire needle, under the aseptic conditions of a transfer chamber.

Table 2.—Composition of vitamin solution used in purified diets for laboratory rearing of the European corn borer.

Vitamin	Concentration[a]
	mg/l
Choline chloride	8,300
i-Inositol	4,600
Calcium pantothenate	850
Nicotinic acid	330
Para-aminobenzoic acid	115
Riboflavin	48
Pyridoxine hydrochloride	37
Thiamine hydrochloride	28
Folic acid	11
Biotin	8
Cobalamin (B_{12})	2

[a]Vitamin solution used at the rate of 8 ml. per 100 g. finished diet.

From 20 to 25 larvae were started on each medium. They were reared in a dark incubator at 40° C. for 8 to 10 days. The larvae (late third stadium) were then weighed, mortality was recorded, and the assay was terminated. On control media, containing no added plant concentrates or resistance chemicals, the larvae attained an average weight of about 20 milligrams, and the incidence of mortality was about 10 percent. Each assay experiment included one control diet, and it was often desirable also to include a diet containing a standard amount of pure RFA or a standardized plant concentrate as a basis for resistance comparisons. In cases where dosage-response curves were plotted, approximately linear regressions resulted when log percent inhibition was plotted against log concentration. Probit plots did not yield linear regressions. Resistance activities of pure chemicals were expressed as the molar concentrations producing 50 percent inhibition (I_{50}).

For routine rearing and the maintenance of a continuing culture of borers, the basal diet (tables 1 and 2) was used. The larvae were reared in individual shell vials, as described above, in a dark incubator at 30° C. The larvae reached pupation at 15 to 21 days of age. The incidence of diapause was negligible. Pupae were transferred to a cloth-covered wire screen cage for emergence, mating, and reproduction. A wax-paper surface was provided for oviposition. By this rearing method, it has been possible to keep a thriving population of borers available for experimental work. We have maintained such a population through nine generations, although growth and reproduction declined after the seventh generation. For plant resistance studies, however, the larvae employed were never more than two generations removed from a field population.

Penicillium Bioassay of Resistance Factors.—It has proved convenient to use the fungus *Penicillium chrysogenum* (NRRL 1951) as a substitute for the European corn borer in routine bioassays. The fungal assay involved culturing *Penicillium* spores for 72 hours on agar media to which plant concentrates or resistance chemicals had been added. Resistance-factor activity was measured as inhibition of colony growth, expressed as percentage reduction of colony diameter compared to the diameter of untreated control colonies. The fungal assay has proved to be much faster, less laborious, and statistically superior to the corn borer assay.

The basal culturing medium was an aqueous

2 percent agar containing 1 percent peptone and 6 percent strained honey. Plant concentrates and chemicals to be assayed were prepared in a manner similar to that of the borer assay. Test solutions were added to the media at the expense of the water volume normally used, and at levels resulting in 1 gram of medium being equivalent to either 1 or 2 grams of fresh plant tissue. The media were made up in 50 ml. volumes, sterilized by autoclaving, and divided between two sterile petri dishes. After cooling and gelling, the plates were inoculated with 1 milliliter of fungal spore suspension containing 12 to 18 spores per milliliter (spore count determined by hemocytometer prior to final dilution). In order to obtain an even distribution of spores over the surface of the agar, it was necessary to manipulate the plates by hand until the inoculum wetted the entire surface. The plates were then placed on a level table for 24 hours at 24°–26° C., at the end of which time they were inverted to allow drainage of excess surface moisture. Seventy-two hours after inoculation, the diameters of five single colonies were measured in each dish. Each treatment was represented by two Petri dishes and, therefore, 10 colony diameter measurements. Under these conditions, unhibited control colonies usually averaged about 10 mm. in diameter. The results obtained by this assay technique were sufficiently reproducible to make an 8-percent inhibition of growth statistically significant.

Penicillium chrysogenum spores used in the assay procedure were obtained from 7-day-old slant cultures on the basal medium. The slant cultures were streaked from a standard soil spore suspension. Perpetuating a standard strain by inoculating new slants from old slants was not satisfactory, as the incidence of aberrant colonies increased markedly after several generations.

RESULTS AND DISCUSSION

The substitution of *Penicillium chrysogenum* colonies for borer larvae in corn resistance assays involved the assumption that the responses of the two organisms were comparable to a measurable degree. The validity of this assumption has been tested in detail. The responses of the two organisms to different concentrations of 6-methoxybenzoxazolinone indicated a similar sensitivity (Beck and Stauffer 1957). The statistical characteristics of the two assay systems are such that the superiority of the fungal assay is apparent (table 3).

Obviously, any responding organism might be made the basis for the bioassay of a given chemical substance. The requirements for comparability of assay organism are that the responses be susceptible to quantitative estimation and that the thresholds and ranges of response not be grossly dissimilar. From these standpoints, *Penicillium* has proved to be a good substitute for the borer in assays of Resistance Factor A. Similar parallelism of response is demonstrable in borer and fungal assays of RFC activity. Although RFB has not been isolated or identified, the response data presented in an earlier paper (Beck and Stauffer 1957) indicate that the responses of the two organisms were also similar in this instance.

One important difference between fungal and insect bioassays is that fungal assays are not complicated by behavioral effects that might influence the results of an insect assay. In studies of the role of plant chemicals in host-plant resistance, separation of behavioral from physiologica

Table 3.—Characteristics of bioassays of 6-methoxybenzoxazolinone (RFA), using *Penicillium chrysogenum* and European corn borer larvae.

RFA (M)	Response			F value	LSD (%I)		Regression	
	Average	%I	s[a]		0.05	0.01	log slope	Chi[2]
				Penicillium chrysogenum				
	mm.							
0.0000	10.0	0.0	5.2					
0.0006	8.9	10.6	9.3					
0.0012	7.7	23.4	6.8	186.74[c]	7.4	9.9	0.944	1.353
0.0024	2.1	78.6	10.0					
				European corn borer				
	mg.							
0.0000	16.1	0.0	29.4					
0.00085	13.6	15.5	28.5					
0.0017	9.8	39.1	28.3	11.82[b]	21.0	28.0	0.824	4.570
0.0026	8.0	50.3	20.4					
0.0034	5.3	65.1	17.9					

[a]Standard deviation in percent response.
[b]F value significant at the 0.01 level of probability.
[c]F value significant at the 0.001 level of probability.

effects may be quite difficult (Painter 1958). The use of a microorganism as a substitute for the insect in question may be an aid in distinguishing the two responses, particularly in assays of crude plant concentrates that may contain repellents and feeding deterrents as well as growth inhibitors. The effects of pure compounds on growth and feeding behavior of the borer have been separated, however, without resorting to substitute bioassay organisms (Beck 1960).

An extensive series of chemicals related to benzoxazolinone have been tested for growth-inhibitory effects against newly hatched European corn borer larvae and *Penicillium crysogenum*. The detailed findings concerning the biological activity of these substances will be presented in a subsequent paper; the extent of parallelism observed between the responses of the two organisms is what concerns the present consideration. Three series of compounds were tested: (1) substituted benzoxazoles; (2) substituted benzothiazoles; and (3) substituted monophenols (table 4). Activity was expressed as the molar concentration resulting in 50 percent growth inhibition (I_{50}). *Penicillium* proved to be the more sensitive assay organism in all three series, in that the I_{50} values were lower, and the response to changes in molecular structure was usually more pronounced. Coefficients of correlation were calculated, using the I_{50} values obtained. As shown in the table of data, there were significant correlations between the responses of borer and fungus to compounds of the benzoxazole and benzothiazole series. In the case of the phenols, no meaningful correlation was detected. The fungus was quite sensitive to a wide range of phenolic compounds, whereas borer growth was inhibited only by very high concentrations of most of the phenolics tested.

The relative insensitivity of the borer to phenols, compared to that of *Penicillium*, represents a limiting factor in the use of the fungus as a substitute assay organism. Many phenolic compounds occur in plant tissues (Bonner 1950, Fairbairn 1959), and in assays of crude plant concentrates fungal growth might be strongly inhibited by phenols in amounts having no inhibiting effects on borer growth. These results indicate that the fungal assay involves a degree of uncertainty as to whether or not all of the apparent resistance-factor activity detected in crude plant concentrates has any pertinence to host plant resistance to the insect. Such uncertainty can be reduced by employing purified plant extracts, and can be largely eliminated through the use of pure compounds isolated from the plant tissue in question.

These limitations notwithstanding, we have investigated the feasibility of using both borer and fungus as assay organisms in host-resistance problems involving plant species not normally utilized by the borer. Larvae of the European corn borer are polyphagous feeders, feeding readily on a wide variety of plant species (Caffrey and Worthley 1927, Hodgson 1928, Bottger 1940), and are not dependent on plant-borne feeding stimulants for the initiation and maintenance of feeding (Beck 1956c). *Penicillium chrysogenum* is not a plant pathogen, and displays very general nutritional requirements. For these reasons, it was felt that these organisms might be of value as substitute assay forms in the identification of resistance factors in plant species other than corn. The validity of such substitutions would be dependent upon a number of factors, however: (1) the resistance under study must be caused by chemical growth inhibitors, rather than by physical, phenological, or behavioral factors; (2) a correlation must be demonstrable between assayed resistance-factor activity and the growth and survival of insect species normally infesting the plant species and varieties involved; and (3) the inhibitory effects of isolated and identified "resistance factors" on the growth of the infesting insect species must be at least qualitatively demonstrable under conditions in which the resistance-factor concentrations approximate that found in the plants studied.

Table 4.—Comparison of growth responses of *Penicillium chrysogenum* and European corn borer larvae to purified media containing different analogs of benzoxazolinone.

Chemical: / Organism:	Benzoxazoles		Benzothiazoles		Monophenols	
	Penicillium	Borer	*Penicillium*	Borer	*Penicillium*	Borer
I_{50} (M) range						
low:	0.00013	0.0012	0.00002	0.0008	0.00002	0.003
high:	0.0077	0.024	0.0095	0.010	0.008	0.020
Correlation coefficient:	r=0.921[b]		r=0.669[a]		r=0.102	

[a]Correlation significant at the 0.05 level of probability.
[b]Correlation significant at the 0.01 level of probability.

Under the conditions described above, it should be possible to conduct meaningful experimental investigations of host-plant resistance in spite of the absence of satisfactory methods of culturing many phytophagous insects under laboratory conditions. Insects such as leafhoppers and aphids have proved to be highly refractive to culturing techniques, but can be held for several days under conditions allowing at least crude assay tests. Such tests might be sufficient to satisfy condition number 3, above, and to allow qualitative or semiquantitative estimation of resistance activity of chemicals isolated from host plant tissue.

Using the European corn borer and *Penicillium chrysogenum* as substitute assay organisms, crude concentrates of varieties of potato, cabbage, alfalfa, wheat, and barley were assayed. The presence of growth inhibitors was detected in all cases, with the response of the fungus being generally similar to that of the borer (table 5). assay results similarly showed variety 12804 to be much more resistant than the others and Comanche to be the most susceptible. The fungal assays did not show such a relationship, however. Virtanen et al. (1956) reported the occurrence of 6-methoxybenzoxazolinone in wheat seedlings, and the study of Refai et al. (1956) on wheat resistance to Hessian fly did not eliminate the possibility that 6-methoxybenzoxazolinone might be involved. The assay data of table 5 do not indicate that this substance was responsible for the observed inhibition of growth. Were 6-methoxybenzoxazolinone responsible, inhibition of fungal growth should have been much higher than that observed.

Crude concentrates of barley caused high levels of growth inhibition in both borer and fungus. Varietal differences were not manifested. Dicktoo is rated as being more resistant to greenbug, *Toxoptera graminum* (Ron), than is the variety Reno (R. H. Painter, personal communication).

Table 5.—Effect of crude concentrates of different plant species and varieties on the growth of *Penicillium chrysogenum* and the European corn borer.

Plant	Variety	Percent inhibition (%I) of growth			
		1 g. tissue/g. medium		2 g. tissue/g. medium	
		Penicillium	Borer	*Penicillium*	Borer
Wheat	Commanche	12.6[b]	17.9	22.8[b]	42.5[a]
Wheat	Pawnee	12.6[b]	22.2	29.1[b]	61.1[b]
Wheat	Ponca	18.0[b]	10.2	32.9[b]	65.6[b]
Wheat	12804	16.2[b]	65.2[b]	29.8[b]	73.1[b]
Alfalfa	Vernal	23.0[b]	81.0[b]	39.8[b]	100.[b]
Barley	Reno	66.0[b]	64.3[b]	83.8[b]	88.8[b]
Barley	Dicktoo	61.4[b]	60.0[b]	79.4[b]	92.7[b]
Potato	Red Warba	35.5[b]	72.0[b]	58.8[b]	88.2[b]
Cabbage	———	22.7[b]	47.0[a]	44.2[b]	75.8[b]
Coefficient correlation		r=0.418		r=0.688[a]	

[a]Statistically significant at the 0.05 level of probability.
[b]Statistically significant at the 0.01 level of probability.

At concentrations of 1 gram of plant tissue (extracted) per gram of medium, the responses of the two organisms did not display a significant degree of correlation. At least two factors appeared to contribute to the lack of correlation: (1) three of the four wheat varieties failed to cause significant inhibition of borer growth, with the fourth (12804) inhibiting strongly; and (2) all four wheat varieties caused low-level inhibition of fungal growth, with the response to variety 12804 being similar to responses to the others.

It is of interest to note that of the wheat varieties tested, Comanche is rated the most susceptible and 12804 the most resistant to Hessian fly, *Phytophaga destructor* (Say) (B. S. Miller, personal communication). The corn borer

Several growth-inhibiting compounds have been isolated and identified from varieties of cabbage, alfalfa, and potatoes. All of the chemicals so obtained have been proved to inhibit the growth of the two assay organisms. What, if any, role these substances might play in plant resistance to insects and pathogens normally infesting the plants involved has yet to be determined.

ACKNOWLEDGMENTS

It is with pleasure that the writers acknowledge their indebtedness to Professors Byron S. Miller and Reginald H. Painter, of Kansas State University, for the wheat and barley samples used in this study.

REFERENCES CITED

Beck, S. D. 1950. Nutrition of the European corn borer, *Pyrausta nubilalis* (Hbn.). II. Some effects of diet on larval growth characteristics. Physiol. Zool. 23: 353–61.

1953. Nutrition of the European corn borer, *Pyrausta nubilalis* (Hbn.). III. An unidentified dietary factor required for larval growth. Jour. Gen. Physiol. 36: 317–25.

1956a. The European corn borer, *Pyrausta nubilalis* (Hbn.), and its principal host plant. I. Orientation and feeding behavior of the larva on the corn plant. Ann. Ent. Soc. America 49: 552–8.

1956b. The European corn borer, *Pyrausta nubilalis* (Hbn.), and its principal host plant. II. Influence of nutritional factors on larval establishment and development on the corn plant. Ibid. 49: 582–8.

1956c. Nutrition of the European corn borer, *Pyrausta* nubilalis (Hbn.). IV. Feeding reactions of first instar larvae. Ibid. 49: 399–405, 510.

1957a. The European corn borer, *Pyrausta nubilalis* (Hbn.), and its principal host plant. IV. Larval saccharotropism and host plant resistance. Ibid. 50: 247–50.

1957b. The European corn borer, *Pyrausta nubilalis* (Hbn.), and its principal host plant. VI. Host plant resistance to larval establishment. Jour. Ins. Physiol. 1: 158–77.

1960. The European corn borer, *Pyrausta nubilalis* (Hbn.), and its principal host plant. VII. Larval feeding behavior and host plant resistance. Ann. Ent. Soc. America 53: 206–12.

Beck, S. D., E. T. Kaske, and **E. E. Smissman.** 1957. Quantitative estimation of the resistance factor 6-methoxybenzoxazolinone in corn tissue. Jour. Agric. and Food Chem. 5: 933–5.

Beck, S. D., J. H. Lilly, and **J. F. Stauffer.** 1949. Nutrition of the European corn borer, *Pyrausta nubilalis* (Hbn.). I. Development of a satisfactory purified diet for larval growth. Ann. Ent. Soc. America 42: 483–96.

Beck, S. D., and **J. F. Stauffer.** 1950. An aseptic method for rearing European corn borer larvae. Jour. Econ. Ent. 43: 4–6.

1957. The European corn borer, *Pyrausta nubilalis* (Hbn.), and its principal host plant. III. Toxic factors influencing larval establishment. Ann. Ent. Soc. America 50: 166–70.

Bonner, J. 1950. Plant Biochemistry. New York: Academic Press, Inc.

Bottger, G. T. 1940. Preliminary studies of the nutritive requirements of the European corn borer. Jour. Agric. Res. 60: 249–57.

Caffrey, D. J., and **L. H. Worthley.** 1927. A progress report on the investigations of the European corn borer. U. S. Dept. Agric. Bull. 1476.

Fairbairn, J. W. 1959. The Pharmacology of Plant Phenolics. New York: Academic Press, Inc.

Hodgson, B. E. 1928. The host plants of the European corn borer in New England. U. S. Dept. Agric. Tech. Bull. 77.

Ishii, S. 1949. Studies on the host plants of the cow pea weevil (*Callosobruchus chinensis* L.). VII. Botyu Kagaku 13: 32–37.

Lipke, H., and **G. Fraenkel.** 1955. The toxicity of corn germ to the mealworm, *Tenebrio molitor*. Jour. Nutrition 55: 165–78.

Loomis, R. S., S. D. Beck, and **J. F. Stauffer.** 1957. The European corn borer, Pyrausta nubilalis (Hbn.), and its principal host plant. V. A Chemical study of host plant resistance. Plant Physiol. 32: 379–85.

Painter, R. H. 1958. Resistance of plants to insects. Ann. Rev. Ent. 3: 267–90.

Refai, F. Y., E. T. Jones, and **B. S. Miller.** 1955. Some biochemical factors involved in the resistance of the wheat plant to attack by the hessian fly. Cereal Chem. 32: 437–51.

Smissman, E. E., J. B. LaPidus, and **S. D. Beck.** 1957a. A corn resistance factor. Jour. Org. Chem. 22: 220.

1957b. Isolation and synthesis of an insect resistance factor from corn plants. Jour. Amer. Chem. Soc. 79: 4697–8.

Virtanen, A. I., A. Aura, and **T. Ettala.** 1957. Formation of benzoxazolinone in rye seedlings. Suomen Kemist. B 30: 246.

Virtanen, A. I., P. K. Hietala, and **O. Wahlroos.** 1956. An antifungal factor in maize and wheat plants. Suomen Kemist. B 29: 143–4.

DIPTERA: NEMATOCERA—BRACHYCERA by D. Elmo Hardy. Insects of Hawaii, vol, 10, xii+368 pp., illus. University of Hawaii Press, Honolulu, 1960. $7.00.

This is the first of four volumes to be devoted to the Diptera of Hawaii, and it is a fine beginning. A check list of the Nematocera and four of the seven families of Brachycera gives the distribution by islands and the overall range of the 152 valid species or subspecies included in this volume. Forty of these, as well as one genus and one subgenus, are new to science. Introductory matter includes sections on the history of dipterology in Hawaii, a discussion of certain nomenclatural problems, morphology, economic importance and techniques. All the Hawaiian families of Diptera are keyed and the 13 (not 14 as given in the preface) families are treated in detail with keys, descriptions, excellent illustrations, and biological and distributional notes. This volume, like the rest of the series, provides very interesting data for the zoogeographer as well as anyone interested in the fauna of the State itself. Approximately one-third of the Diptera of Hawaii have been introduced, and the endemic species are concentrated in a relatively few genera.

There is little to criticize in the work. It is unfortunate that while the late F. I. van Emden is correctly associated with the Commonwealth Institute although he worked at the British Museum, the dipterists at the U.S. National Museum are not indicated as being employed by the Agricultural Research Service. There are two glaring typographical errors in family names in the check list. Figure 1 would have been much better placed in or after the section on morphology rather than awkwardly breaking the section on new nomenclatural changes. Finally, the statement on the hybridization of *Aedes aegypti* and *A. albopictus* is very misleading. It implies that only one fertile egg was produced by such a cross although Bonnet actually reared 376 adults in five generations from an original crossing of 4 female *aegypti* and 8 male *albopictus*. All of these adults were phenotypic for *aegypti* and it was only by backcrossing hybrid females with *albopictus* males that he got one adult that was phenotypic for *albopictus*.

Alan Stone
Entomology Research Division
U. S. Department of Agriculture

MORPHOLOGY OF THE REPRODUCTIVE SYSTEMS AND MATING IN TWO REPRESENTATIVE MEMBERS OF THE FAMILY NOCTUIDAE, PSEUDALETIA UNIPUNCTA AND PERIDROMA MARGARITOSA, WITH COMPARISON TO HELIOTHIS ZEA[1]

PHILIP S. CALLAHAN[2] AND JOAN BEGGS CHAPIN[3]
Louisiana State University, Baton Rouge

ABSTRACT

The gross morphology of the reproductive system is described and illustrated for the male and female of *Pseudaletia unipuncta* (Haw.) and *Peridroma margaritosa* (Haw.), and comparisons are made with *Heliothis zea* (Boddie). Each of these species is a member of a separate subfamily, and their adults are, respectively, long-, medium-, and short-lived. The method of inserting the spermatophore is described, and both morphological and functional reproductive characteristics are compared and summarized. Mating percentages are given for feral populations.

Investigations of reproductive morphology and mating in the family Noctuidae have in the past followed the classical descriptive approach in which little attention was given to the relationship between structure and function in the reproductive pattern of Lepidoptera. In order to integrate the reproductive anatomy of the imago with the mating behavior and process of spermatophore formation a more dynamic approach is necessary.

With this approach in mind, three species of Noctuidae have been chosen for detailed study of reproduction and reproductive behavior. They are representative of species of three subfamilies which have short, medium, and long lives, respectively. The morphology and reproductive behavior of the first one, the short-lived corn earworm, *Heliothis zea* (Boddie), have been described (Callahan 1958a, 1958b). The two species presented in detail in this paper are the variegated cutworm, *Peridroma margaritosa* (Haw.),[4] representative of a medium-lived species, and the armyworm, *Pseudaletia unipuncta* (Haw.), representative of a long-lived species.

Reproduction and, consequently, the reproductive potential of a lepidopterous population, are in the main dependent upon the following factors: (1) Food available during the larval and imago stages; (2) The egg potential of the ovarian germarium and sperm potential at emergence; (3) The percentage of mating among individuals of the population; and (4) Length of life of the individuals. This paper is not primarily concerned with the first two factors, other than to note the obvious fact that the latter two are affected by variations in the former. The fourth factor, length of life, is considered only insofar as it is used as the criterion for comparisons between the three species.

What, then, is the importance of the third factor to reproductive potential and species population dynamics? Mayr (1942) stated that individual fertilization is the exclusive method of reproduction of all land animals and that they all have two characteristics in common: (1) The sexually active individuals have a certain "cruising radius" and actively seek each other, and (2) Fertilization is internal (mammals, insects, etc.) or at least individual (amphibia, and so forth). These two characteristics of land animals directly affect the percentage of mating, and thus the reproductive potential, of insects and other animals. Variations of the first characteristic, which affect reproductive potential, include area of the "cruising range" or spatial separation and degree of attractibility of the sexes to each other. Variations of the second characteristic include any factors, morphological or functional, which would promote or prevent mating. The term "mating" is used in the more complete sense of successful fertilization of the egg by sperm and should not be confused with copulation, which is a union of sexes that may or may not be successful in producing progeny.

TECHNIQUES

The mechanics of spermatophore insertion were studied by techniques of serial morphology as described by Callahan (1958b). Sixty specimens of *Pseudaletia unipuncta* and twenty-five *Peridroma margaritosa* were dissected in saline solution at the beginning of, during, and after copulation. Sperm transmission was also studied at this time,

[1]Especial thanks are due to the National Science Foundation for financial support made available under Grant G-3980 (Nocturnal behavior and reproduction of Lepidoptera in the family Noctuidae); to Joan Landry Lasack and Dorothy Meakin for preparation of several of the accompanying illustrations; to Dr. Dan Clower for allowing us access to the imagos of his armyworm cultures. For sending armyworm specimens for examination we are also indebted to Dr. G. S. Breeland, University of Tennessee; Dr. George Decker, University of Illinois; Dr. Herbert Knutson, Kansas State University; Dr. T. R. Pfrimmer, Mississippi State University; and Dr. L. H. Rolston, University of Arkansas.

Accepted for publication March 28, 1960.

[2]Associate Professor of Entomology.

[3]Research Assistant.

[4]After this paper was submitted for publication we were advised by Dr. E. L. Todd (personal communication) that the previously used name *Peridroma margaritosa* (Haw.) had been corrected to *Peridroma saucia* (Hbn.).

but is the subject of a future paper on the histology of the reproductive tracts.

The percentage of mating for populations of *P. unipuncta* and *P. margaritosa* have been determined by methods similar to those used for *H. zea* (Callahan 1958a, 1958b). For purposes of comparison in this paper it may be stated that *H. zea* is a rather short-lived moth (average of 6.9 days), with a complicated method of spermatophore transfer and an extremely stable percentage of 50 to 60 percent mating for populations thus far studied (Callahan 1958a, 1958b).

LENGTH OF LIFE OF THE IMAGO OF *P. unipuncta* AND *P. margaritosa*

Zalensky (1938) gave the length of life of the imago *P. margaritosa* (*Rhyacia saucia*) as 10 to 15 days when fed honeydew, and 8 to 10 days with no food. Wadley (1921) gave the length of life of *P. margaritosa* as from 8 to 13 days when fed on sugar water. Forty adults caged by the authors and fed sugar water lived from 6 to 15 days with an average of 8.7 days.

Breeland (1958) gave the average life of the armyworm as 10 days, with some moths living as long as 27 days. One hundred armyworms kept by the authors lived from 6 to 20 days, with an average life of 11.1 days, when fed on sugar water. In general it might be said that caged adults of *H. zea* live in the neighborhood of 7 days, *P. margaritosa* 9 days, and *P. unipuncta* 11 days. It might be well to point out that, generally speaking, the females of *P. unipuncta* (Breeland 1958) and of *H. zea* (Callahan 1958a) lived an average of 1 day longer than the males. These averages are for free-flying, caged adults. It is possible, by suspending the moths in holders as described by Ditman et al. (1933) and Callahan (1958a) and feeding them sugar water, to increase considerably the length of life. Earworms have been kept alive up to 25 days, with an average of 16.8 days for 17 females. Two *P. margaritosa* were kept alive 31 days, and an armyworm for 42 days.

REPRODUCTIVE SYSTEMS OF THE MALES OF *P. unipuncta* AND *P. margaritosa*

Generally speaking, the male reproductive tracts of these two species and the earworm are quite similar. There have been no descriptions of the morphology of the internal reproductive ducts of male *P. unipuncta* or *P. margaritosa*, although both Franclemont (1951) and Breeland (1958) have accurate drawings of the external genitalia of *P. unipuncta*.

Testes.—The testes of both *P. unipuncta* (fig. 1A) and *P. margaritosa* (fig. 2A) are paired and so closely united that they appear as a single round organ enclosed in a common scrotum. In this respect they fall into Cholodkovsky's (1884) class D (*Pieris*) group testes, as does the earworm. The most obvious difference between these organs is in the color of pigment. The *P. unipuncta* testes are of a deep crimson color, whereas those of *P. margaritosa* are cream-colored. The testes lie dorsally in the third abdominal segment.

Seminal Vesicles.—The seminal vesicles are swollen enlargements of the vas deferens, and in *P. unipuncta* (fig. 1B) cross each other at the point of entrance into their respective testes. This is also true of *H. zea* (Callahan 1958b). The seminal vesicles of *P. margaritosa* (fig. 2B–B) are closely united but do not cross. In most specimens there is a slight constriction at the anterior end, and also a definite narrowness which divides the seminal vesicles into anterior and posterior enlargements.

Vas Deferens.—The vasa deferentia of *P. unipuncta* (fig. 1C) and *P. margaritosa* (fig. 2C) are paired narrow tubes from 16 to 20 mm. in length. Each vas deferens extends from the posterior end of its respective seminal vesicle to a point midway on one of the branches of the ductus ejaculatorius duplex (figs. 1E and 2E). These ducts are capable of extreme distention and, while ordinarily they measure 0.25 mm. in diameter, they expand to six times their normal width as sperm bundles pass down the ducts. Dissections of copulating specimens of all three Noctuidae show that the sperm bundles have not separated in their movement from the testes through the seminal vesicles and vas deferens.

Ductus Ejaculatorius Duplex.—The ductus ejaculatorius duplex (figs. 1E and 2E) is a paired glandular reservoir for both the opaque accessory gland substance and the sperm bundles leaving the vas deferens. When empty they normally measure 1 mm. in diameter and 6 to 8 mm. in length. In all three species there is a distinct S-shaped bend (fig. 1K, insert) at the junction between the paired duplex and the paired accessory glands, which are cephalad extensions of these glandular reservoirs. Musgreave (1937) termed the duplex the "paired gland system" and demonstrated on a histological level a partition, "presumably broken down during copulation," between the paired glands and their extensions, the accessory glands, in the lower species *Anagasta kuhniella* (Phycitidae). Dissections of all three species immediately before and during copulation show that the paired duplex becomes filled with a mixture of the opaque accessory gland substance and sperm bundles. This mixture may extend the duplex to 1.5 mm. in diameter and 8 to 10 mm. in length. In young moths the secretion of the accessory gland can be distinguished from that of the duplex by its brighter whitish color.

Accessory Glands.—The accessory glands are shown separated in *P. unipuncta* (fig. 1D). In all three species they are normally joined and held tightly together by fine tracheae as pictured for *P. margaritosa* (fig. 2D). Shortly before copulation when the glands are full they distend

to approximately 0.5 mm. in diameter throughout their entire length. After copulation when nearly empty they may decrease in width at their anterior end (fig. 1D) until they become almost threadlike. They may range from 90 to 110 mm. in length, and constitute the longest duct in the tortuously entwined reproductive tract.

Ductus Ejaculatorius Simplex.—The ductus ejaculatorius simplex is a rather general term used by morphologists to designate the single duct extending from the duplex to the endophallus. Callahan (1958b) pointed out that in *Heliothis zea* this duct consists of two distinct morphological areas separated by an area where the frenum (lock) of the spermatophore is formed. The more cephalad portion was termed the primary segment of the ductus ejaculatorius simplex and constitutes the area where the spermatophore precursors are elaborated, while the caudal portion was referred to as the cuticular segment and constitutes the area where the spermatophore precursor is moulded into the resilient spermatophore prior

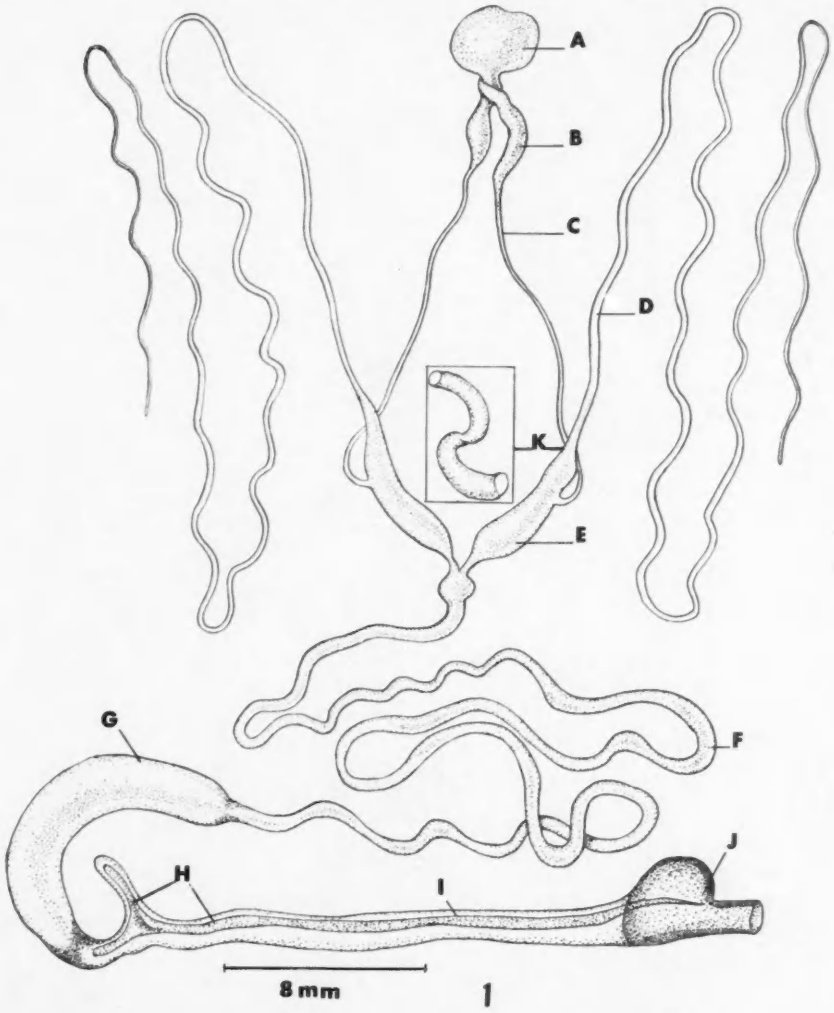


FIG. 1.—Male reproductive system of *Pseudaletia unipuncta*. A, testes; B, seminal vesicles; C, vas deferens; D, accessory gland; E, ductus ejaculatorius duplex; F, primary segment of ductus ejaculatorius simplex; G, heavy muscular area of cuticular segment of ductus ejaculatorius simplex; H, frenum end of spermatophore within the shoehorn lateral extension at anterior end of cuticular segment of ductus ejaculatorius simplex; I, cuticular segment of ductus ejaculatoris simplex containing collum of spermatophore; J, caecum of aedeagus; K, (insert), S-shaped bend between accessory gland and ductus ejaculatorius duplex.

to deposition in the female bursa copulatrix.

Primary Segment of the Simplex.—Musgreave (1937) referred to this portion as the "unpaired gland system" and differentiated four histological segments separated by four intermediate cellular areas in *Anagasta kuhniella* (Phycitidae). Norris (1932), in the same species, differentiated four glandular areas rather than eight, while Stitz (1901) divided this single duct of Lepidoptera into three main segments and several intermediate areas and maintained that it produced several kinds of secretions. There is considerable evidence (*Heliothis zea*, unpublished data) that leaves little doubt in the authors' minds that this segment, with its various secreting areas, is functional in elaborating the spermatophore precursors, and that the accessory glands (Khalifa 1950 notwithstanding) produce a substance which

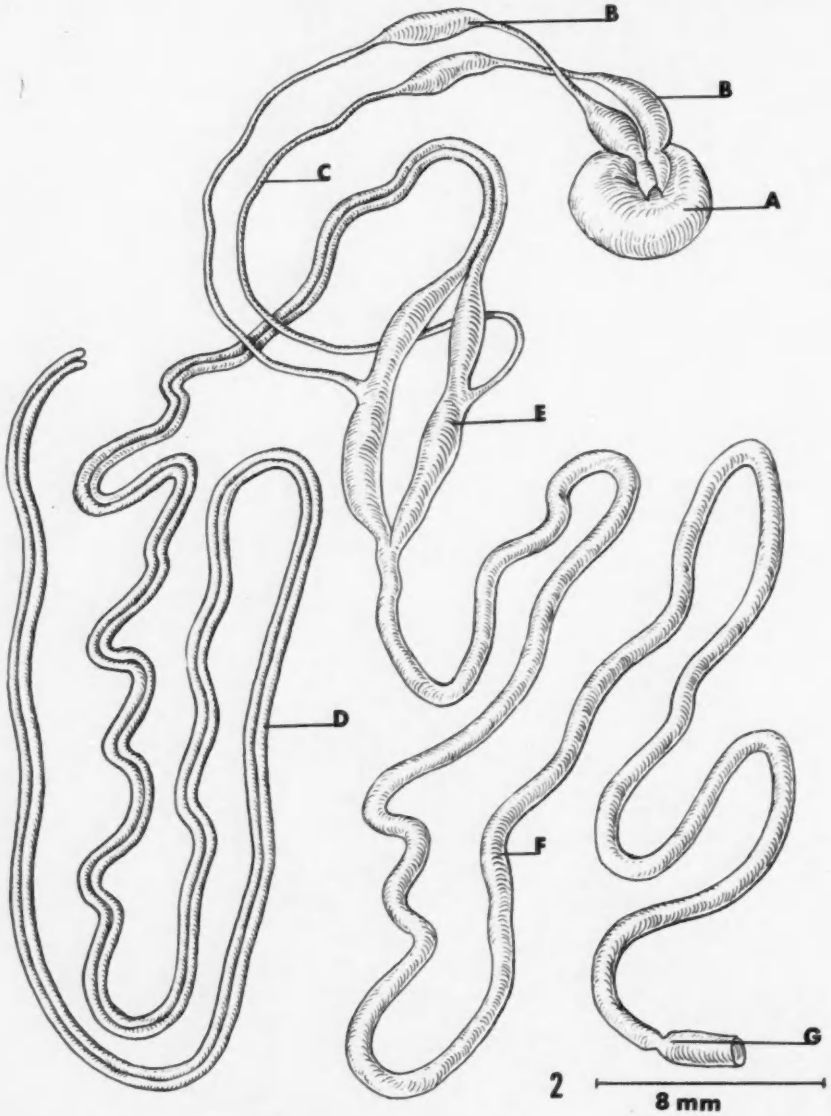


FIG. 2.—Male reproductive system of *Peridroma margaritosa*. A, testes; B, seminal vesicles; C, vas deferens; D, accessory glands; E, ductus ejaculatorius duplex; F, primary segment of ductus ejaculatorius simplex; G, heavy muscular area of cuticular segment of ductus ejaculatorius simplex.

intiates the rhythmic movements of the female reproductive ducts that result in sperm transmission. There is conclusive evidence that in *Rhodnius prolixus* (Hemiptera) (Davey 1958) the male accessory secretion sets up rhythmic contractions in the female ducts. Davey points out that this may be true of other spermatophore-forming insects.

From a gross morphological standpoint (figs. 1F and 2F) there is little variation between the primary ducts of the three species. The primary simplex is a rather thin-walled tube ranging in width from 0.5 to 1.5 mm. depending on the amount of luminar secretion. The length varies from 45 mm. in a small *P. unipuncta* specimen up to 90 mm. in a large *P. margaritosa* specimen. In young moths four very distinct areas can be observed on the basis of their secretions alone.

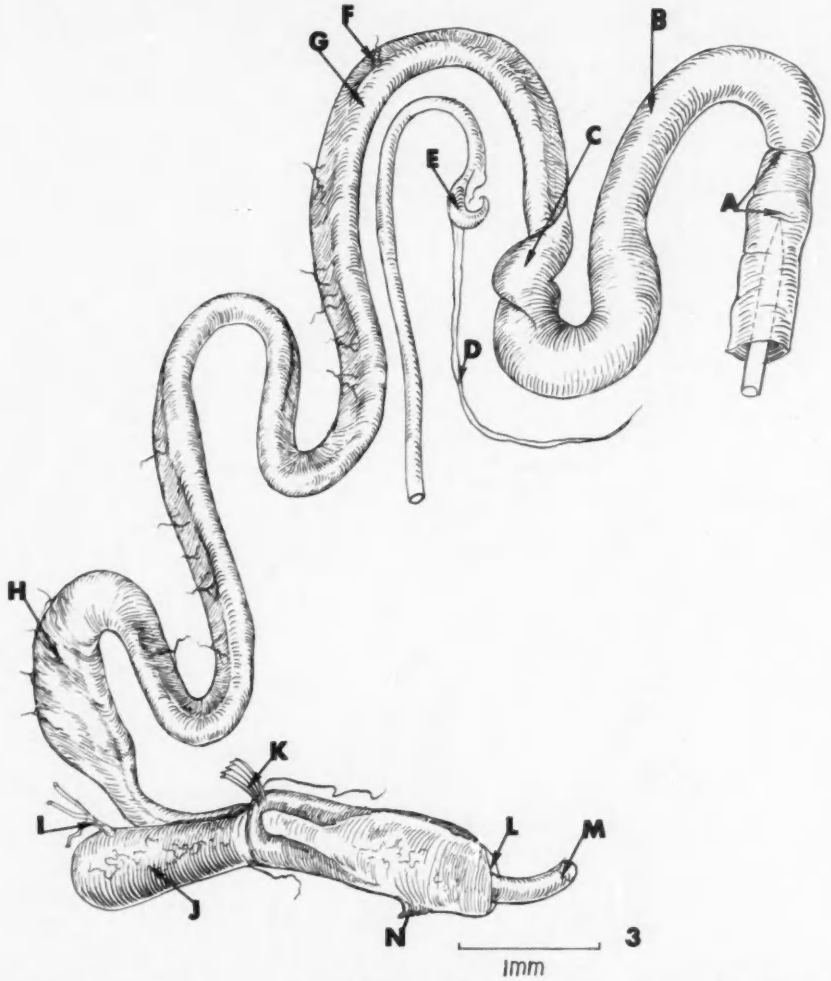


FIG. 3.—Aedeagus and cuticular segment of the ductus ejaculatorius simplex of *Peridroma margaritosa*. A, Non-muscular primary portion of ductus ejaculatorius simplex and constriction at junction of this area of the organ with the heavy muscular frenum area of the cuticular section; B, heavy muscular area of the cuticular section. The spermatophore is moulded below this point after it is pulled from the primary segment by the action of this muscle. D represents the residue of the spermatophore after it has been constricted off from the spermatophore precursor of the primary segment; C, area where frenum (E) and aperture of spermatophore are formed; F, area of transverse muscle of cuticular segment of ductus ejaculatorius simplex; G, cuticular tube of ductus ejaculatorius simplex; H, broadened band of lateral transverse muscle at base of aedeagus; I, tracheal branches into caecum of aedeagus; J, caecum of aedeagus; K, retractor muscle insertion on the aedeagus; L, aedeagus, inverted secondary gonopore; M, spermatophore collum emerging from gonopore; N, keellike carina.

AREA OF FRENUM FORMATION AND CUTICULAR SEGMENT OF THE DUCTUS EJACULATORIUS SIMPLEX

Here, in the most caudal portion of the reproductive ducts, we find the greatest morphological variation between species of Noctuidae. The variations are so distinct that specimens may be separated at a specific level by comparisons of the cuticular segment of the ductus ejaculatorius simplex. This organ receives the precursor substances from the primary segment and moulds them into the distinct, characteristic spermatophore of each species. In order to test the hypothesis that the aedaegus and cuticular ductus ejaculatorius simplex are good taxonomic criteria, of the reliability of these organs as a taxonomic criteria.

The area of frenum formation and cuticular simplex of *Heliothis zea* has been described in detail (Callahan 1958b), and the reader is referred to that paper for comparative purposes. Based upon that work and what is herein presented, there is little doubt that the elongated cuticular segment of the ductus ejaculatorius simplex (16 to 20 mm. long in the three species) represents in the family Noctuidae an evolutionary advancement over the less complex ejaculatory duct of the lower Phycitidae. Comparisons with the work of Norris (1932) on the Genera *Anagasta*

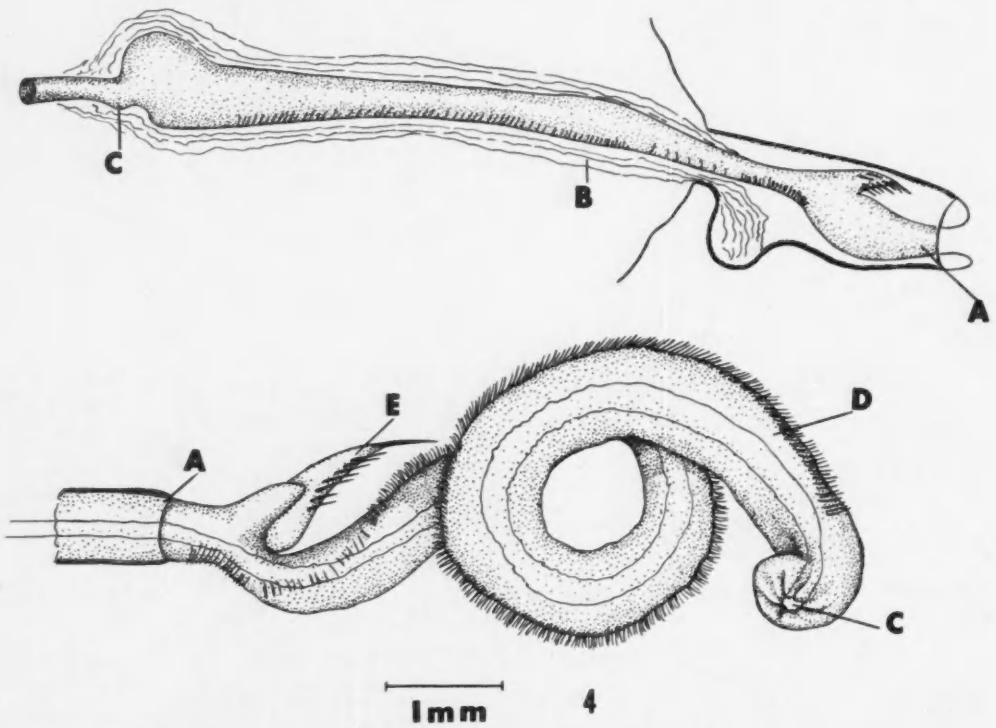


FIG. 4.—Bifurcate endophallus of *Pseudaletia unipuncta*, inverted and pulled back (top), and everted (bottom). A, junction of endophallus with posterior edge of aedeagus, secondary gonopore at normal inversion; B, endophallic tracheae (anteriorly these retract into the bulbous caecum of the aedeagus); C, junction of cuticular duct of cuticular section of the ductus ejaculatorius simplex with the endophallus (primary gonopore, top; endophallus everted, bottom, so that primary gonopore has become same as secondary gonopore); D, everted primary arm of endophallus, showing dense row of cornuti; E, everted secondary arm of endophallus, showing row of large cornuti and terminal spine.

28 species were dissected and drawn by research assistants. The drawings were numbered and given to the principal researcher. With no knowledge whatsoever of the species, he was able to group the various specimen drawings into categories which turned out to be the generic categories. This was felt to be unbiased evidence and *Plodia* (Phycitidae) and Musgreave (1937) on *Anagasta* substantiate this contention.

The primary portion of the simplex of both *P. unipuncta* and *P. margaritosa* terminates caudally with a slight constriction (fig. 3A). This area marks the termination of the glandular, nonmuscular primary simplex. The most cephalad

portion of the muscular cuticular simplex is the area of frenum formation of the spermatophore. It is represented in both species by a thick heavy duct of circular striated muscle about 2 to 3 mm. long (figs. 1G, 2G and 3B). In *H. zea* this area is looped around by a portion of the remaining cuticular simplex (Callahan 1958b). This organ is homologous to that which Norris (1932) called the bulbous ejaculatorius in *Anagasta* and *Plodia* species. The bulbous ejaculatorius of the latter species is a cuticular duct about 0.5 mm. long with heavy muscular walls.

Following the muscular organ is the area where the actual moulding of the frenum (lock) on the spermatophore tip takes place. In *P. unipuncta* this organ takes the shape of a lateral "shoe-horn" appendix (figs. 1H and 13J). This characteristic outgrowth of the cuticular simplex is responsible for the "shoe-horn"-shaped frenum of the spermatophore of *P. unipuncta* (fig. 11A). In *P. margaritosa* it takes the form of a curved "half-moon" swelling (fig. 3C). The hooklike frenum (fig. 3E) of the *P. margaritosa* spermatophore is moulded within this organ. As in *H. zea* the

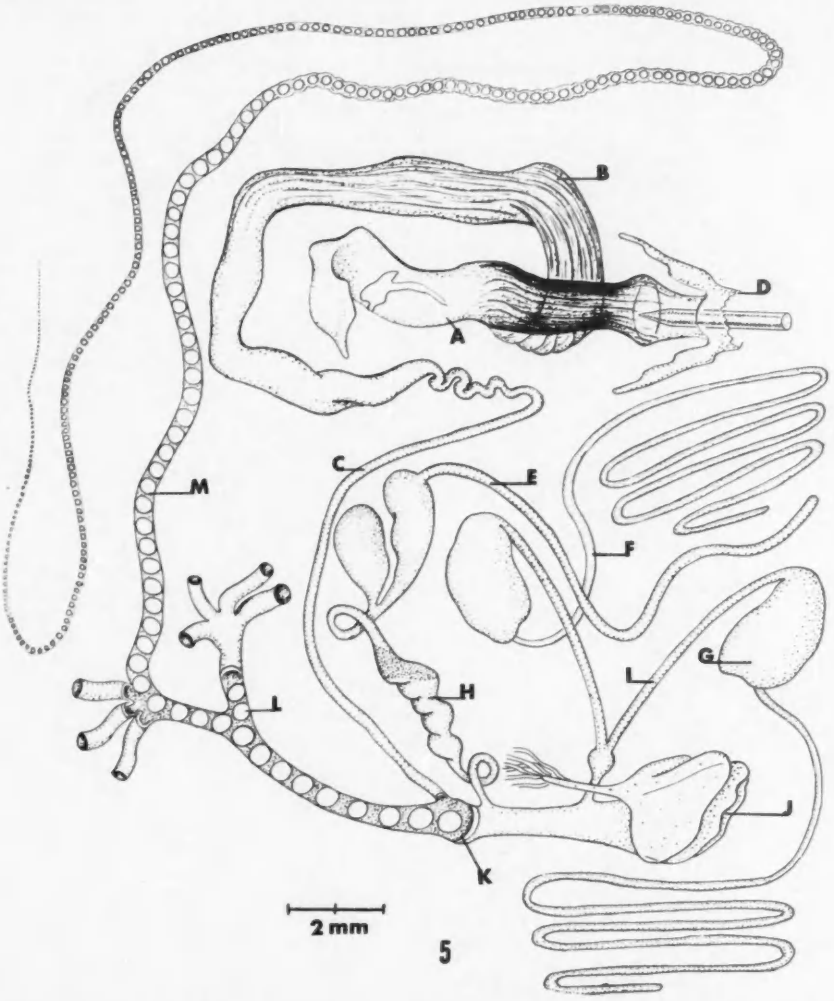


FIG. 5.—Dorsal view of the female reproductive system of *Pseudaletia unipuncta*. A, corpus bursae of bursa copulatrix; B, cervix bursae of bursa copulatrix; C, seminal duct; D, pin inserted through ostium bursae into ductus bursae; E, spermathecal gland; F, accessory glands (glandulae sebaceae); G, paired accessory gland reservoirs; H, bilobed spermatheca and spermathecal duct, showing convoluted and sclerotized area; I, duct to paired accessory glands (glandulae sebaceae); J, glandular tissue surrounding the oviduct within the papillae anales of ovipositor; K, vestibulum; L, calyx of the unpaired oviductus communis; M, single ovariole of the paired ovaria.

remainder of the simplex of both species consists of a cuticular tube (figs. 1I and 3G) bounded on one side by a lateral band of transverse striated muscle fibers (fig. 3F). At the caudal base of the cuticular simplex of *P. margaritosa* these bands of muscle fiber (fig. 3H) are considerably wider, being 1 mm. across, than in the other species.

In all probability the "inflated chamber" and "hollow horn" organs of the lower *Anagasta* and *Plodia* species are homologous to the area where the frenum is moulded in the Noctuidae. Norris (1932) did not ascribe any function to the "hollow horns" of the male duct but pointed out that *Anagasta* and *Plodia* spermatophores are moulded with horns at their aperture ends which match the "hollow horn" organ. These "hollow horns" are at the base of the aedeagus so that there is no long cuticular duct between the bulbous ejaculatorius with the conjoining "hollow horns" and the base of the aedeagus. Norris could distinguish species by the placement and arrangement of these horns on the spermatophore, and since the spermatophore aperture is between the horns it is not unreasonable to ass me that the frenum of the Noctuidae spermatophore and the horns of the lower species are homologous. It would seem that in the lower families the area that represents the thick duct of circular striated muscle and

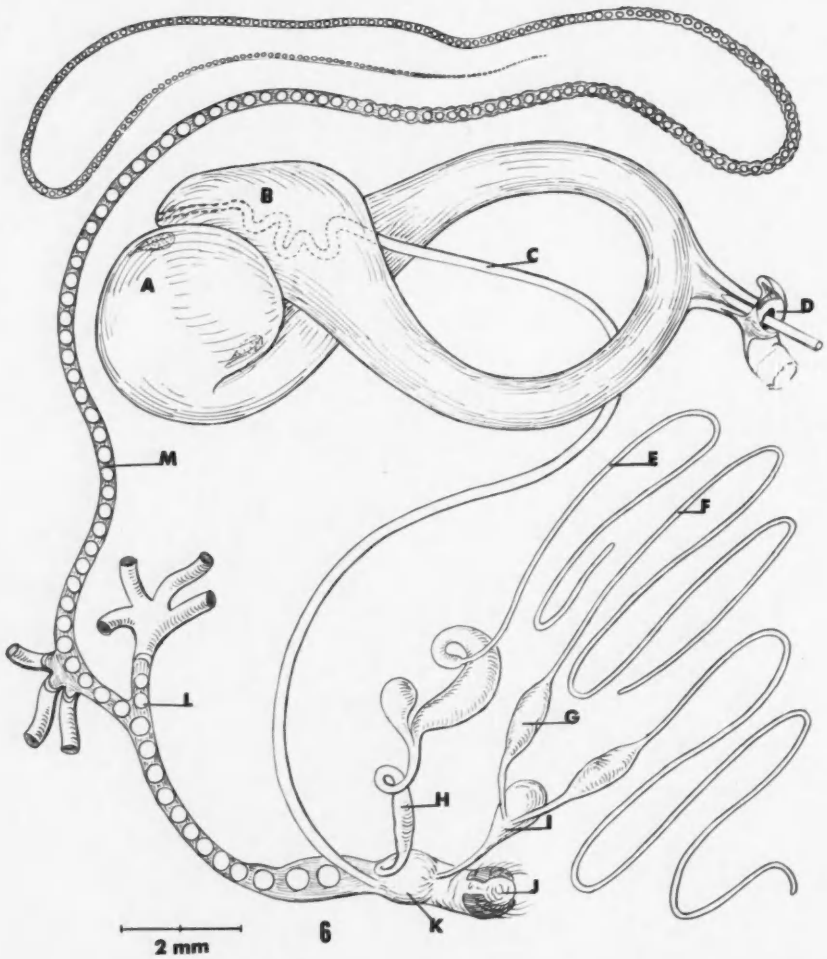


FIG. 6.—Dorsal view of the female reproductive system of *Peridroma margaritosa*. A, corpus bursae and paired signa; B, cervix bursae; C, seminal duct; D, pin inserted through ostium bursae into cervix bursae; E, spermathecal gland; F, accessory glands (glandulae sebaceae); G, paired accessory gland reservoirs; H, bilobed spermatheca and spermathecal duct, showing swollen, nonsclerotized area; I, duct of accessory glands and single reservoir; J, ovipositor and papillae anales; K, vestibulum; L, calyx of the unpaired oviductus communis; M, single ovariole of the paired ovaria.

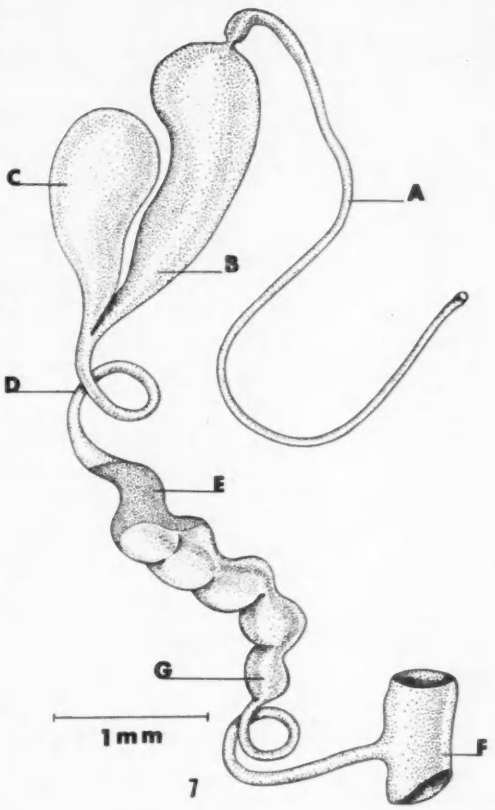
conjoined area of frenum formation of Noctuidae had been moved posteriorly until it is represented by the bulbous ejaculatorius and "hollow horn" area right at the base of the aedeagus, the intervening area of cuticular duct with lateral muscle (figs. 3G and F) not being present.

Aedeagus and Endophallus.—The organs of copulation in these three moths may be said to represent the extremes of specialized differentiation, the aedeagus and endophallus of *P. margaritosa* representing one of the more simple of the Noctuidae and that of *P. unipuncta* one of the more complicated, with *H. zea* falling between.

Both *P. unipuncta* and *P. margaritosa* have well-developed aedeagal caeca. The caecum of the Noctuidae aedeagus may take the form of a club-shaped, heavily sclerotized, blind pouch extending cephalad from the aedeagus into the body cavity, as in *P. margaritosa* (fig. 3J), or of a round ball cephalad of the main body of the aedeagus, as in *P. unipuncta* (fig. 1J). There are other variations, but among 28 species studied these are the most common. The caecum has been thought to be mainly for muscle attachment (Kusnezov 1915), but this is not its primary function. In all species so far studied the heavy anterior protractor muscle of the aedeagus inserts on or behind the caecum, but the heavy posterior retractor muscle inserts dorsally on the aedeagus proper just caudad of the caecum (Forbes 1939), *P. margaritosa* (fig. 3K). In many species, and the genus *Heliothis* is a good example, there is no caecum at all. The main function of the caecum is to serve as a storage place for the retracted endophallus, its muscles and the long unbranched tracheae that help evert the endophallus (unpublished data). In the case of *H. zea*, which has no caecum, the endophallus, muscles and tracheae are folded in accordion pleats along the entire length of the long (8 mm.), narrow aedeagus. In the case of *P. unipuncta* the endophallic muscles and tracheae are coiled like a ball of twine inside the caecal bulb, and in the case of *P. margaritosa* they are retracted into a caecal club. The source of the everting tracheae of the endophallus is an extremely heavy tracheal arm which bifurcates as it goes into the body cavity, and which enters the caeca (fig. 3I) of both species anteriorly. The cuticular portion of the ductus ejaculatorius simplex of *P. margaritosa* (fig. 3G) enters the aedeagus dorsally and just cephalad of the junction of the main aedeagal body and the caecum. As in *H. zea*, the cuticular lining of this duct is a continuation of the inverted cuticular endophallus, which is an inverted continuation of the aedaegus. The lateral transverse muscles (figs. 3F, H) of the simplex end at the junction of the simplex and aedeagus.

The cuticular portion of the simplex of *P. unipuncta* enters the ventral anterior portion of the bulbous caecum (figs. 1I, J). As in the other species, the lateral transverse muscle stops here while the cuticular duct continues on inside to meet the endophallus.

The aedeagus of *P. margaritosa* (fig. 3L) is only a little over 1 mm. long and is actually sclerotized only on its dorsal and ventral surfaces, the lateral surfaces being characteristically membranous. At the more posterior end of the ventral sclerotized area is a keel-like carina (fig. 3N). The endophallus of *P. margaritosa* lacks cornuti and is extremely simple being only an 8 to 10 mm., membranous invagination of the aedeagus. Obviously this long endophallus with



7

FIG. 7.—Spermatheca of *Pseudaletia unipuncta*. A, spermathecal gland; B, large lobe (utriculus) of spermatheca; C, small lobe (lagena) of spermatheca; D, upper loop of ductus receptaculi (spermathecal duct); E, sclerotized area of spermathecal ductus receptaculi; F, vestibulum; G, convoluted area and lower loop of ductus receptaculi.

muscles and tracheae could not be stored along the short body of the aedeagus, and it is thus retracted into the caecum.

The aedeagus of *P. unipuncta* is also about 1 mm. long from the caecal bulb to the tip, but

is completely sclerotized and bears no carina. It is indeed a simple cylindrical tube, but the inverted endophallus is extremely complex and the armyworm has by far the most complicatey mechanics for spermatophore insertion of and species so far studied.

The endophallus is pictured inverted, but pulled back, in fig. 4 top, and everted as during copulation (fig. 4 bottom). Completely inverted, the secondary gonopore is at the point (A top) where the endophallus joins the aedeagus. As the endophallus everts the primary gonopore (C top) approaches closer and closer to the

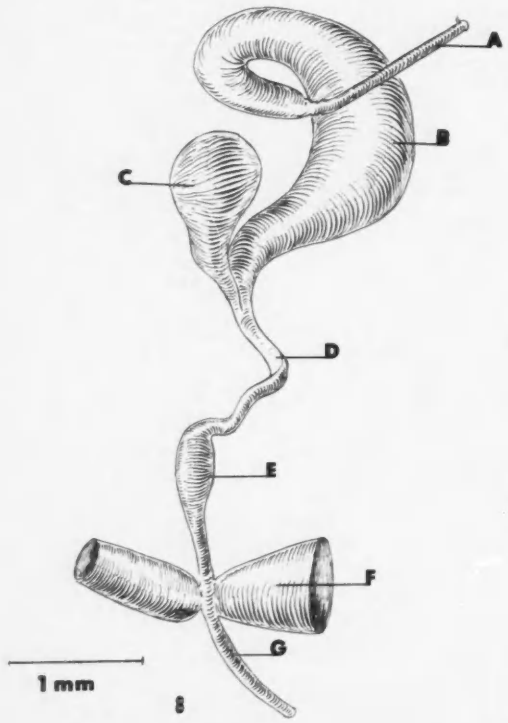


FIG. 8.—Spermatheca of *Peridroma margaritosa*. A, spermathecal gland; B, large lobe (utriculus) of spermatheca; C, small lobe (lagena) of spermatheca; D, twisted portion of ductus receptaculi (spermathecal duct); E, distended portion of ductus receptaculi; F, vestibulum; G, seminal duct.

secondary gonopore until both become the same at complete expansion of the endophallus (C bottom). This holds for all species studied.

The endophallus of *P. unipuncta* is bifurcate, one arm being the long, 8 to 10 mm., main endophallus, which has a brush line of very fine cornuti from one end to the other (D bottom), and the other arm being a short lateral branch with 11 to 13 long heavy cornuti (E bottom). The end cornuti of this arm is in reality a heavy spine almost 1 mm. long. It rests at the very apex of the triangular lateral arm. Fig. 4B top shows the long, unbranched tracheae that follow along the endophallus. These are retracted into the caecal bulb, where they terminate at the main tracheal arm. As in the other species, they lay between the walls of the endophallus and the cuticular duct of the simplex at complete eversion.

FEMALE REPRODUCTIVE SYSTEMS OF *P. unipuncta* AND *P. margaritosa*

The female reproductive system of *P. unipuncta* has never been described. Both Franclemont (1951) and Breeland (1958) gave excellent drawings of the bursa copulatrix of this moth. Williams (1948, fig. 4) described in detail the reproductive system of a moth he termed *Leucania unipuncta*. The species *unipuncta* has since been put in the genus *Pseudaletia* (Franclemont 1951) and is supposedly the noctuid described by Williams. His paper is, however, contradictory to what the authors found. Williams' drawing of the reproductive tract of *Leucania unipuncta* is obviously that of *P. margaritosa*. His description of *P. margaritosa* (*Leucania unipuncta*) omits many details, so *P. margaritosa* will be redescribed herein.

Bursa Copulatrix.—The bursa copulatrix of *P. unipuncta* (fig. 5 dorsal view) is quite heavily sclerotized. Heavy, sclerotized ridges extend the length of the ductus bursae (D pin, drawing), and anteriorly up the corpus bursae (A) about halfway. The last 3 to 4 mm. of the corpus bursae is a membranous sac in which the corpus of the spermatophore lies. There are no signa. The cervix bursae (B) extends laterally from the left side and crosses ventrally to the main sclerotized portion of the corpus bursae. It extends laterally about 2 to 3 mm., then makes a right-angle bend and runs cephalad along side of the corpus bursae. For about 7 to 9 mm. the cervix bursae is also heavily sclerotized with deep, pleated ridges, especially at the inside edge of the organ. At a point just above the anterior extension of the corpus bursae, the cervix bursae makes another right-angle bend and curves U-shaped around the corpus bursae. This latter 6- to 8-mm. portion of the cervix bursae is membranous.

The bursa copulatrix of *P. margaritosa* (fig. 6 dorsal view) is U-shaped and only the ductus bursae (pin, drawing) is sclerotized, the corpus bursae and cervix bursae being membranous. Dorsally the saclike cervix bursae (B) rests on the corpus bursae (A). The cervix bursae is from 6 to 8 mm. long. The corpus bursae is from 8 to 10 mm. long, but not as wide or saclike and pliable as the cervix bursae. Laterally on the corpus bursae are two teardrop-shaped signa.

Seminal Ducts.—The seminal duct connects between the anterior termination of the cervix

bursae and the vestibule of the ovipositor. In both species (figs. 5C and 6C) the seminal ducts are convoluted at the point where they join the cervix bursae. They range from 16 to 20 mm. long, depending on the specimen's size. The seminal duct of *P. unipuncta* joins the vestibule (fig. 5K) of the oviduct at an average of 0.3 mm. anterior to the junction of the spermathecal duct with the vestibule. In the case of *P. margaritosa* the seminal duct may enter the vestibule (fig. 6K) immediately opposite the spermathecal duct. In most Noctuidae so far studied by the authors, it is usual for the seminal duct to attach at the vestibule on the opposite side and from 0.2 to 0.5 mm. cephalad of the spermathecal duct. The point of attachment is variable, however, and specimens of both species have been observed with the attachment anywhere from right at the spermathecal duct to 0.8 mm. cephalad of the duct.

Spermatheca.—The spermatheca of *P. unipuncta* consists of a tubular spermathecal gland from 14 to 18 mm. long (fig. 7A), a large lobe, 2 mm. long (B), and a small lobe, 1.3 mm. long (C). These have been termed the utriculus and lagena respectively (Weidner 1935). The spermathecal gland enters the utriculus at its apex. Just below the point where these two lobes come together, 1 mm. of the ductus receptaculi is thrown into a loop (D). About 0.5 mm. below this characteristic loop, 1.5 mm. of the ductus receptaculi expands to a width of about 0.4 mm. The top portion of this expanded area is heavily sclerotized (E), while the bottom posterior portion is convoluted (G). The last 2 mm. of the duct makes a second loop before it continues on to join the vestibulum of the oviduct (F).

The spermatheca of *P. margaritosa* consists of the same general anatomical areas but in no detail does it resemble *P. unipuncta*. The spermathecal gland (fig. 8A) ranges from 9 to 14 mm. long. It also joins the apex of the utriculus (B), but the top of the utriculus makes a complete loop so that the gland passes laterally across the side of the utriculus before continuing cephalad in the body cavity. The lagena (C) is shorter (1 mm.) than that of *P. unipuncta* and tends to be rounder at the top. The ductus receptaculi may be looped or slightly twisted (D) for about 2 mm. of its length. The duct then enlarges and is clublike and swollen (E) for about 1 mm. of its length. The ductus receptaculi narrows where

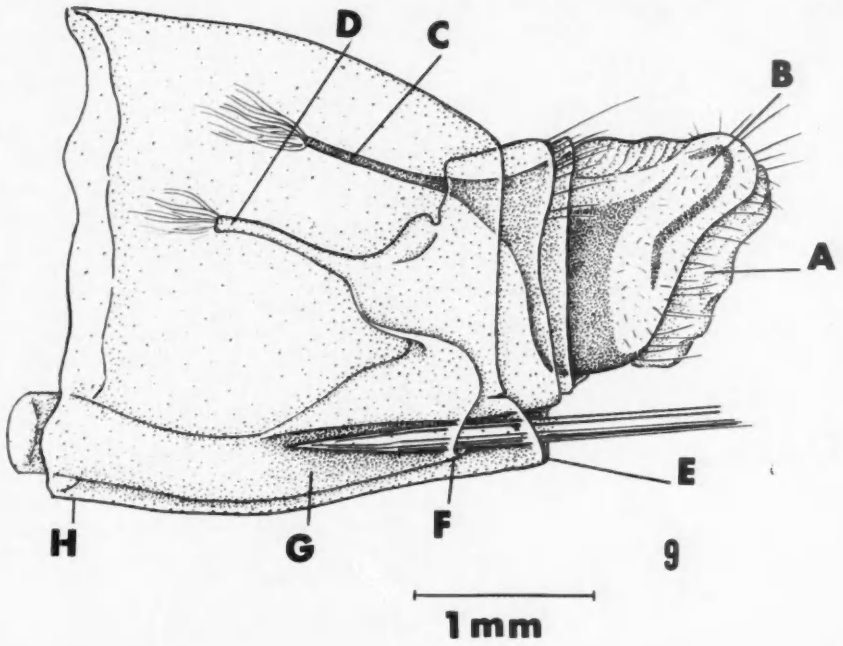


FIG. 9.—Ovipositor of *Pseudaletia unipuncta*. A, glandular tissue surrounding oviduct at posterior extremity of ovipositor; B, papillae anales of ovipositor; C, apophyses posteriores of 9th–10th segment; D, apophyses anteriores of 8th segment; E, pin inserted in sinus vaginalis ventrad of the lamella postvaginalis; F, pin inserted in ostium bursae dorsad of the lamella antevaginalis; G, ductus bursae; H, seventh sternite.

it enters the vestibule (F) opposite the seminal duct (G).

Accessory Glands.—In *P. unipuncta* the bifurcate ducts (fig. 5I) of the accessory gland reservoirs (G) unite close to the junction of the main reservoir duct with the oviduct. At this point there is a slight enlargment. The main duct enters the oviduct about 2 mm. caudad of the vestibule and is about 1 mm. long. The bifurcate ducts range from 6 to 7 mm. long. The reservoirs when filled with secretion are roundish and bend back laterally along their respective ducts. The accessory glands (F) attach to the apex of the reservoirs and range from 21 to 23 mm. long.

In *P. margaritosa* the main duct of the accessory gland reservoirs is about 2 mm. long and swells into a large single reservoir (fig. 6I) connecting the bifurcate ducts. The main duct enters the oviduct about 1.5 mm. caudad of the vestibulum. The bifurcate ducts do not enter the apex of the fused terminal germarium where oögonia are formed, for a suspensory ligament. None of the 90 noctuids so far studied by the authors of this paper has a suspensory ligament. The oviductus communis extends from the vestibulum (figs. 5K and 6K) to the oviductus lateralis (figs. 5L and 6L) and ranges from 3 to 3.5 mm. in length. Including the vestibulum, the oviductus communis in both species may hold from 8 to 12 fully matured eggs. The oviductus lateralis of both species is 1 mm. in length from its first bifurcation to the calyx where the paired ovaries each branch into four ovarioles (figs. 5M and 6M). The oviductus lateralis of both species may contain from one to three mature eggs. The paired ovaries of both species range from 65 to 75 mm. long and make five complete loops, each time reversing direction for about 10 to 11 mm. and turning back laterally along each other. In a matured moth the first 15 mm., the first loop and part of

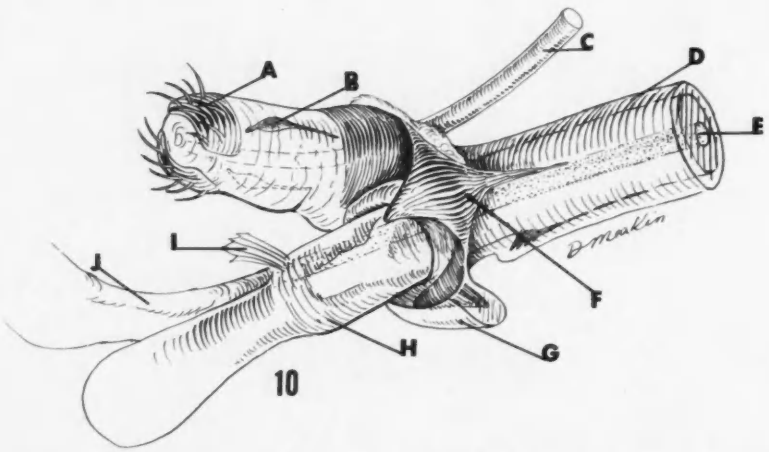


FIG. 10.—Aedeagus of male *Peridroma margaritosa* inserted in ostium bursae of female. A, papillae anales of extended ovipositor; B, apophyses posteriores of 9th–10th segment; C, oviduct; D, outer wall of ductus bursae of bursa copulatrix; E, endophallus and cuticular duct of cuticular segment of ductus ejaculatorius simplex pulled along by eversion; F, apophyses anteriores of 8th segment; G, sclerotized fold (lamella antevaginalis) ventrad of ostium bursae; H, aedeagus; I, retractor muscle insertion on aedeagus; J, cuticular tube of cuticular portion of ductus ejaculatorius simplex, and broadened band of transverse muscle.

single reservoir but enter close together at the midpoint of this reservoir. The bifurcate ducts are only about 1 mm. long and open into the two club-shaped reservoirs (G). The accessory glands (F) range from 20 to 22 mm. long and join the reservoirs at their apices.

Ovaries.—The polytrophic type ovaries of both moths are typical of Lepidoptera and neither has a suspensory ligament. Of the noctuid *Agrotis ypsilon* Williams (1948) made the following statement, "Le ligament ovarien (fig. 1A) est fortement développé chez cette espèce." *Agrotis ypsilon* was dissected and no suspensory ligament was found. Williams (fig. 1A) mistook the closely the second, constitutes the pedicle where fully matured eggs are stored. The range of both species is from 30 to 60 eggs per ovariole depending on the reproductive state and age of the moth. Like *H. zea*, these two species will not oviposit unless fertilized, and probably absorb their nonmatured eggs, i.e. eggs without chorion (Callahan 1958b). When close to death *P. margaritosa*, with no spermatophore, have been observed to squeeze out a few nonfertile eggs, but not so for *P. unipuncta*. In both species the second part of the ovarioles, the vitellarium, may hold from 30 to 80 oöcytes plus their trophocytes (nurse cells). This area extends for about 25

to 30 mm. for two and one-half or three loops. It may be distinguished from the pedicle by the fact that there is a slight constriction of the ovariole between each oöcyte plus nurse cell and the next. The remainder of the paired ovaries is the germarium where oögonia are formed. The four germaria of each ovary are tied closely together by connective tissue.

Ovipositor.—The ostium oviductus of *P. unipuncta* is surrounded by a glandular ring of tissue (fig. 9A). This glandular tissue lies between the two flattened, triangular papillae anales (B). Microscopically this tissue is formed of units of large-celled protrusions which throw themselves into scalloped pads around the ostium oviductus. Extending anteriorly from the cephalo-subdorsal edges of the papillae anales are the apodemes for muscle attachment, the apophyses posteriores of the 9th–10th segment (C). The ostium bursae (F pin) is encircled by the sclerotized band of the eighth segment, to which are conjoined at the cephalo-subdorsal edge the apophyses anteriores (D). The sclerotized plate below this segment and ventrad of the ostium bursae (F) which opens into the ductus bursae (G) is termed the lamella antevaginalis and arises in the 7th-8th intersegmental cuticula. The lamella antevaginalis is closely fused to the seventh sternite. Dorsad of the ostium is the lamella postvaginalis which fuses with the eighth sternite plus tergite (above pin), making their separation indistinguishable. In a retracted position the lamella postvaginalis is dorsad and forms the roof of the copulatory chamber, the sinus vaginalis (E) which is bounded ventrally by the lamella antevaginalis and the surrounding seventh sternite (E to H). This whole complex of genital sclerites is termed the sterigma and is retracted into the seventh abdominal segment.

The ostium oviductus of *P. margaritosa* is not surrounded by glandular tissue and the papillae anales (fig. 10A) are not directly connected at their cephalo-subdorsal edges with their apophyses posteriores (B). The ovipositor and papillae anales are rounded and the apophyses posteriores are rather thin sclerites slightly expanded in width posteriorly. These sclerites represent the 9th-10th segment. Conjoined to the cephalo-subdorsal edge of the encircling eighth segment are the apophyses anteriores (F). The aedeagus (H) of the male is pictured inserted in the ostium bursae. Dorsad of the aedeagus can be seen a lip, the lamella antevaginalis. Ventrad of the aedeagus there is a fold in the lamella antevaginalis (G). This characteristic pocket is quite deep (1 to 1.5 mm.) and heavily sclerotized. As in the armyworm, the lamella postvaginalis and lamella antevaginalis arise in the 7th-8th intersegmental cuticula but are so fused to the eighth tergite and sternite and the seventh sternite, respectively, that their boundaries are indistinct.

SPERMATOPHORE

The spermatophore of *P. unipuncta* takes the exact shape of the cuticular simplex of the male with the shoehorn frenum (fig. 11A) being moulded in the lateral appendix. The collum (B) is curved and takes the direction of the female bursa copulatrix (already described) so that the corpus (C) lies in the membranous portion of the corpus bursae while the opposite aperture end is held by the frenum at the junction of the seminal

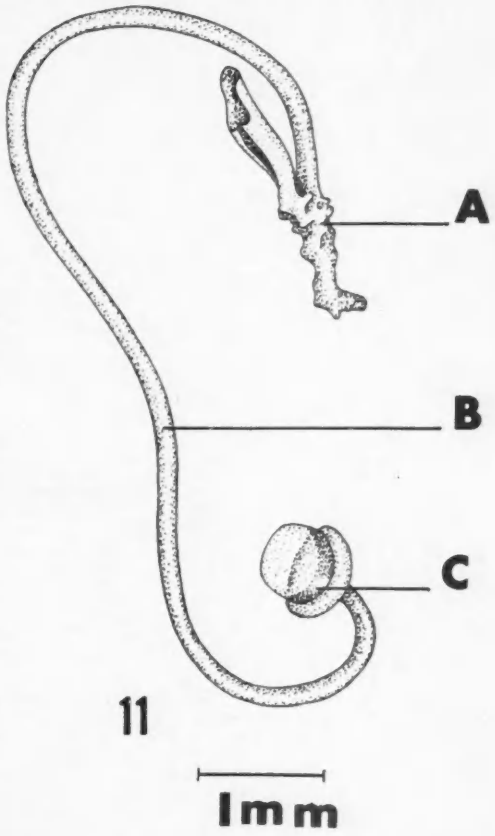


FIG. 11.—Spermatophore of *Pseudaletia unipuncta*. A, aperture end and shoehorn frenum of spermatophore; B, collum of spermatophore; C, corpus of spermatophore.

duct to the cervix bursae. While expanding during insertion, the corpus of the spermatophore appears somewhat acorn shaped as pictured. One hundred spermatophores tested positive for chitin when subjected to the Rollofsen and Hoette chitosan sulphate test (Tracey 1955).

The spermatophore of *P. margaritosa* takes the exact shape of the male cuticular simplex and the collum also takes the direction of the female

bursa copulatrix, with the exception that the collum is bent in a circle at the frenum end (fig. 12B) so that this portion fits as a loop in the saclike cervix bursae. The short hooklike frenum (fig. 3E) of this spermatophore often has a long residue of spermatophore precursor (D) attached at its posterior curve. This residue represents the final portion of the spermatophore that has been constricted off by the heavy muscular area of the cuticular simplex. The corpus of the *P. margaritosa* spermatophore is rounded (fig. 12A) and fits in the corpus bursae between the opposite signa. The spermatophore of this moth is by far the heaviest studied and often appears dark-brownish as compared to the translucent plastic color of the earworm and armyworm spermatophores. Since the earworm (Callahan 1958b) and armyworm spermatophores both contain chitin, those of *P. margaritosa* may also. Immediately following deposition there is a round bulb at the aperture and frenum end of the spermatophore. This represents the state of all three spermatophores (earworm, armyworm and variegated cutworm) within 15 minutes of the completion of copulation. It is herewith termed the cap of the spermatophore and represents a large mass of sperms and accessory fluid formed into a ball between the spermatophore aperture and seminal duct. This cap gradually disappears over a 12-hour period as the sperm move out.

MECHANISMS OF SPERMATOPHORE TRANSFER

Transference in P. unipuncta.—Of the three species so far studied, the armyworm presents by far the most complex method of spermatophore

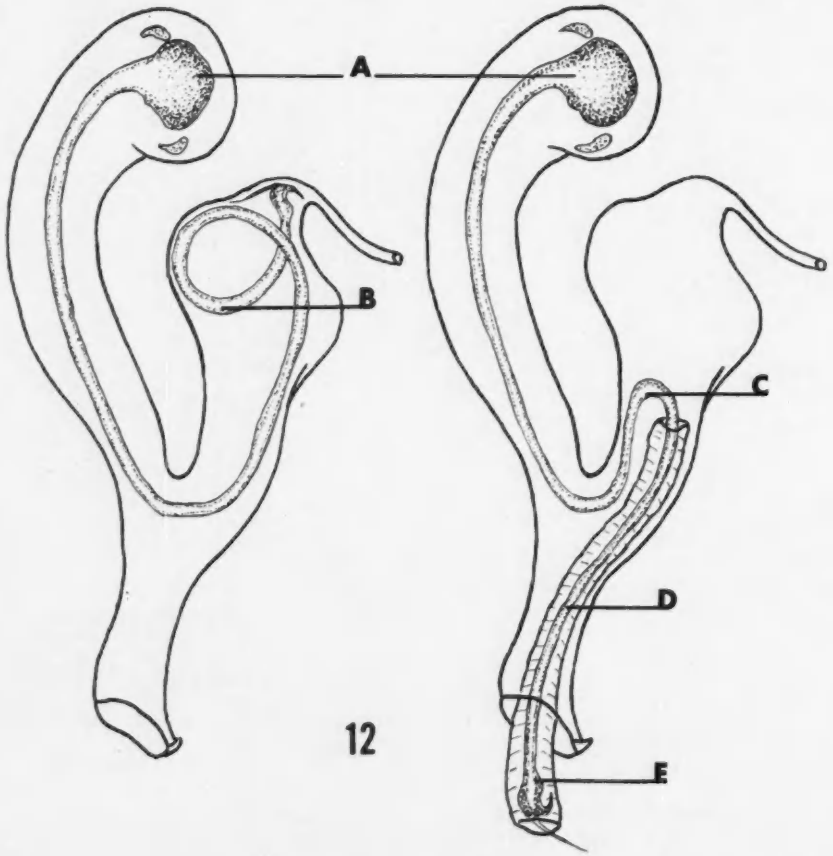


FIG. 12.—Left: final position of *Peridroma margaritosa* spermatophore in female bursa. Right: endophallus everted part-way up cervix bursae and inserting loop. A, corpus of spermatophore oriented in corpus bursae between signa; B, loop of spermatophore collum in cervix bursae; C, collum of spermatophore being fed into cervix bursae by endophallus; D, endophallus everting with contained spermatophore; E, frenum end of spermatophore moving through endophallus.

transference. The earworm (Callahan 1958b) might be said to be intermediate in complexity, and *P. margaritosa* rather simple.

The spermatophore precursor in the form of a partially sculptured but soft rod is drawn from the primary simplex by the action of the heavy muscular area (fig. 1G) of the cuticular simplex. This muscle serves two functions: (1) To draw out the precursor of the spermatophore from the primary simplex and feed it down along the cuticular simplex; and (2) To constrict off the precursor after one complete length, the distance from the area of frenum formation to the corpus, has passed down the cuticular simplex (unpublished data). After the precursor has passed into the cuticular simplex, the lateral muscles of the cuticular simplex (fig. 13I) and of the lateral appendix (J) act on the precursor to mould it into the typical armyworm spermatophore collum with shoehorn frenum. There is no all of its cornuti and the terminal spine on the outside. During the next 15 minutes or so the spermatophore tip, now oriented up to the primary arm, can be seen to swell (F) just behind its terminal pointed tip. This is representative of the period when the tip expands to form the corpus of the spermatophore. Mechanical action is not the whole answer to this corpus expansion and there is, no doubt, a chemical reaction between other substances and the inner walls of the spermatophore that also accounts for expansion (unpublished data). The primary arm of the endophallus at this period lies partially everted in the corpus bursae (D). Here we have a deviation from spermatophore transfer in the earworm, as the endophallus never normally enters the corpus bursae of that insect (Callahan 1958b). As the endophallus continues to evert, the corpus of the spermatophore and part of the collum are fed up into the corpus bursae by the gripping action of

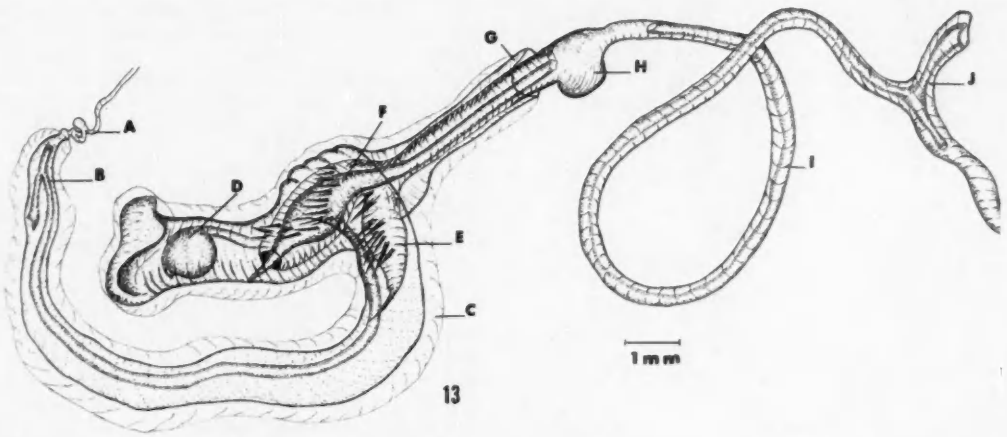


FIG. 13.—Ventral view of bifurcate endophallus of *Pseudaletia unipuncta* inserted in bursa copulatrix of female which contains one spermatophore. A, convolution at junction of seminal duct with cervix bursae of bursa copulatrix; B, aperture end of spermatophore and shoehorn frenum; C, outer epithelial wall of cervix bursae; D, corpus of spermatophore from earlier copulation; E, secondary arm of bifurcate endophallus blocking cervix bursae and showing expanded arm, cornuti, and terminal spine; F, corpus of newly moulded spermatophore beginning to expand within the gradually everting primary arm of the endophallus; G, aedeagus in ostium bursae of female; H, caecum of aedeagus, where tracheae and muscles for endophallic eversion are retracted; I, collum of forming spermatophore within the cuticular segment of the ductus ejaculatorius simplex.

corpus formed on the spermatophore at this time, and the distal end presents only a sharp point. As this pointed tip reaches the caecum of the aedeagus (H), the endophallus (E and F) begins to evert. At this time the male is clasping the female firmly and the short armyworm aedeagus is in the ductus bursae (G) up to the aedeagal caecum. Within the first 20 minutes of copulation the endophallus has everted to the point where part of the cornuti of the primary arm of the endophallus (F) have passed to the outside (from the inside as eversion proceeds) and the secondary arm (E) has completely everted with the endophallic primary arm and the lateral muscles of the cuticular simplex. Before the spermatophore corpus becomes too large for the gonopore (about 50 minutes) the primary arm of the endophallus begins to invert, withdrawing itself from the corpus bursae, and leaving the gradually expanding corpus of the spermatophore in the membranous portion of the corpus bursae. During all this time the secondary arm of the endophallus has been blocking the entrance of the cervix bursae. At about 60 minutes, when the primary arm has inverted back to the point of its bifurcation with the short secondary arm,

the secondary arm retracts itself from the cervix bursae and some rather complicated manipulations occur. The secondary arm moves over to the corpus bursae and works the cornuti of its inside edge and the terminal spine over the spermatophore collum. These heavy cornuti and the terminal spine grip the collum firmly at the point where it bends around and up into the cervix bursae. As the collum is thus held in place in the corpus bursae by the secondary arm, the primary arm again everts, this time being oriented up the cervix bursae which is no longer blocked by the secondary arm. As it everts, its brushlike cornuti grip the remainder of the spermatophore collum and carry it along up the cervix bursae. Obviously, as the endophallus everts up the cervix bursae, the collum will be

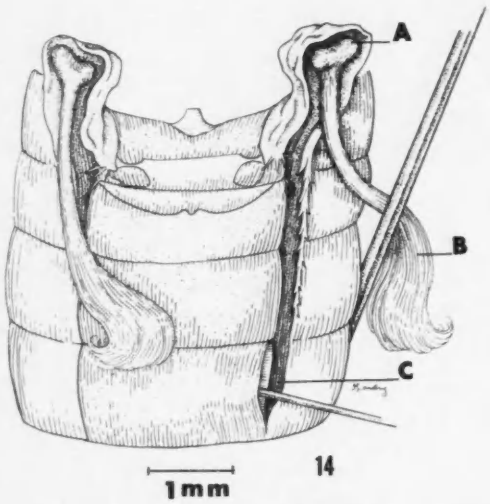


FIG. 14.—Scent brushes ("Strahlapparat") of *Pseudaletia unipuncta* and *Peridroma margaritosa*. A, muscle into which scent-dispersing hairs insert; B, scent-dispersing brush; C, ventral abdominal pockets into which the brushes retract and into which the abdominal scent glands open.

pulled out as it is already anchored in place by the corpus in the corpus bursae and the secondary arm. As it is pulled out from the gonopore it lies in a loop alongside the endophallus. At final expansion when the aperture end comes out the loop is, of course, gone. Like the earworm at complete eversion, the primary gonopore (fig. 4C) has become the same as the secondary gonopore and the cuticular duct of the simplex has been drawn up the center of the endophallus so that at 80 minutes or so (complete eversion) all the brushlike cornuti are on the outside of the primary arm of the endophallus. As in the earworm, the aperture end and frenum are the last to leave the gonopore, and as the primary arm inverts for the second time, retracting itself from the cervix bursae, the frenum and aperture end (fig. 13B) are left in place against the seminal duct (A). The frenum presses against the side of the cervix bursae holding the aperture against the seminal duct. Copulation takes from 80 to 100 minutes.

In the armyworm the endophallic muscles and tracheae retracted into the caecum (H) evert the endophallus. At complete expansion they lie, as in the earworm, between the center cuticular duct of the simplex and the wall of the endophallus. The muscles insert at the base of the cornuti, and the tracheae (fig. 4B) come from a main trunk in the aedeagal caecum and terminate just past the primary gonopore. Pulled backwards and inside out (as in fig. 4 top), so that the cornuti of the primary arm are on the inside, as stored in the normal inverted position, these tracheae can be seen as 40 to 55 unbranched, parallel tubes. Due to the position of the tracheae and their unbranched state, aerostatic pressure is believed to aid the muscle in the expansion of the endophallus. The tracheae of the body cavity are known to be nonresilient, due to the makeup of their coillike taenidia, but endophallic tracheae dissected from the armyworm were easily distended to seven times their normal length and cannot, therefore, be considered nonresilient.

Transference in P. margaritosa.—The spermatophore of *P. margaritosa* is moulded in the cuticular simplex also and the heavy muscular area above the area of frenum formation acts in the same capacity as in the armyworm and earworm. The actual insertion is, however, considerably different and easier to follow, due to the simplicity of the *P. margaritosa* endophallus. As in the armyworm the aedeagus, being quite short, fits only a short distance up the female ductus bursae (fig. 10). While inserted the keellike carina of the aedeagus hooks behind the anterior inner edge of the lamella antevaginalis (G). Since the endophallus lacks cornuti and in essence enters only a membranous saclike bursa, this modification apparently serves to lock the organs together while allowing the endophallus to work in and out of the two parts of the bursa. In the earworm, which also has a somewhat membranous bursa, the expanded cuticular caeca at the junction of the endophallus with the aedeagus (Callahan 1958b) serves to lock the organs together. In the armyworm, with its heavily sclerotized bursa and spined endophallus, any such locking mechanisms would seem superfluous.

Following insertion of the aedeagus the simple endophallus (E) everts into the ductus bursae (D) and orients up the corpus bursae. The sequence is similar to that described for the armyworm, and after the corpus end of the spermatophore has been inserted in the corpus bursae (fig. 12A), the endophallus inverts back to the bifurcation of the bursa and everts again, this time orienting up the cervix bursae (C). The collum of the spermatophore is longer than the cervix bursae

and so, unlike the armyworm, does not lie completely along the cervix bursae but retains the inserting loop (B) in the collum. The seminal duct leaves the cervix bursae at its tip and the retained loop fits, so that the aperture end is left, after the second inversion, close to the seminal duct. The loop tends to act as a spring which holds the frenum close to the seminal duct. The frenum is reduced in this insect and the loop is probably more important than the frenum in holding the aperture in position in such a large saclike area.

In both the armyworm and earworm, the spermatophores are quite resilient during the insertion process; contrarily, in *P. margaritosa* the spermatophore is rigid and springlike from the moment its tip protrudes from the gonopore. This characteristic is so pronounced that during mating the process of insertion can be observed from the insect's exterior. The rigid spermatophore collum being fed into the membranous, saclike bursa shows as a distinct keellike ridge in the abdominal wall. As the process evolves, this ridge can be traced by its movements which correspond to the feeding progression of the collum. It is this rigid springlike characteristic of the *P. margaritosa* spermatophore that enables the simple endophallus to control the insertion of the spermatophore in spite of its lack of cornuti. From this standpoint we must consider the complicated cornuti arrangement of the other two noctuids as playing their most important role after they have everted to the outside of the endophallus. The gripping action of the cuticular simplex muscles is apparently sufficient to draw and feed the spermatophore forward without recourse to action on the part of the cornuti before eversion.

PERCENTAGE OF MATING IN FERAL POPULATIONS

The percentage of mating for the two species was determined by the same methods used for *H. zea* (Callahan 1958b). The only departure from the techniques outlined previously was that light-trapped specimens were preserved in 10% formalin solution rather than 70% alcohol. Structures of formalin-preserved specimens are almost as soft and pliable as those of fresh moths, whereas those of alcohol-preserved specimens become so hard they are difficult to study.

The percentage of mating for 1194 female armyworms of 12 samples from Texas, Louisiana, Arkansas, Mississippi, Illinois and Ohio, from April 23, 1956, to July 23, 1956, was 34.3 percent. The possibility that this low percentage of mating was due to a northward movement on the part of some of the trapped moths could not be overlooked. The armyworm has long been considered "migratory". The range for mating in these samples was from 0% to 97.4%, and because of the extreme variability of these early samples at different latitudes the authors are engaged in a 4-year study of the northward dispersal of this insect.

A more static sample of 805 moths collected from the Baton Rouge light trap from March 9, 1958, to December 20, 1958, yielded a percentage of mating for females of 56.3% (table 1). This percentage compares closely to that of the earworm (table 4); however, when the static and nonstatic populations are combined an average of only 40.6% mating is obtained. The sex ratio was 48.2 males to 51.8 females.

Table 1.—*Pseudaletia unipuncta*, Baton Rouge, La., 1958. Mated moths with spermatophores and nonmated moths falling in three fat-body classifications.

Class of fat body	Number of spermatophores					Total females		Males
	1	2	3	4	5	Mated	Nonmated	
1	22	2				24	62	31
2	24	7	1	1		33	70	111
3	61	67	35	13	2	178	50	246
Total	107	76	36	14	2	235	182	388
	45.5%	54.5%				56.3%	43.7%	48.2%

The catch of *P. margaritosa* at Baton Rouge was considerably lower than that of the armyworm, and in order to get an adequate sample the 1958 and part of the 1959 catches have been lumped together (table 2). The percentage of mating for the females of this sample of 503 was 15%. The sex ratio was 52.4 males to 47.6 females, the reverse of the armyworm. This ratio compares favorably with the earworm (table 4), and in all three insects, for large samples, the range varies closely one way or the other around a ratio of 50/50. The low percentage of mating is suspect, as a single sample of 32 female moths obtained from Shreveport, Louisiana, April 8–17, 1958, showed 81% of them to be mated.

An interesting factor in the mating of both of these species is that the percentage of multiple matings is higher than the percentage for single matings, being 54.5% multiple matings to 45.5% single matings for *P. unipuncta* (table 1) and 56% multiple matings to 44% single matings for *P.*

margaritosa (table 2). This is the reverse of the situation in the earworm (table 4). There is possibly a relationship between the number of multiple matings and the degree of efficiency of the releaser scent-gland mechanisms of the males of the three species. *H. zea* has a scapal scent gland (unpublished data) while both the other moths have abdominal pockets in the first to fourth abdominal segments into which retract long scent brushes (fig. 14B). These are the "Duft-und-Strahlapparat" first described by Stobbe (1912) for certain of the Noctuidae. The latter type of scent brush is found in various species of Noctuidae, with no regard to speciation within genera or even subfamilies. The functioning of these scent brushes has, as of now, never been observed; but, as in the earworm, caged males have always been seen to seek the female so that quite possibly they are releaser glands that serve to initiate the female response. It would seem indicative of the efficiency of such possible releaser glands that 80% to 90% mating of these two species is easily obtained in cages. This is not true of the earworm (Callahan 1958a).

The fat body classification is indicative of the age of the moth (Callahan 1958b). It should be noted (tables 1 and 2) that most of the mated moths of both species are in the old (class 3) group while the nonmated individuals are mainly young (class 1) or medium aged (class 2). The fact that random samples of moths are being obtained from the light trap is supported by the variability in age of the trapped individuals. There are fewer young (class 1) specimens of both male and female moths being taken. This certainly indicates that the trap is not attracting a freshly emerged, biased sample as might be suspected in the case of these two insects, especially in regard to the low percentage of mating in *P. margaritosa*.

Table 2.—*Peridroma margaritosa*, Baton Rouge, La., 1958–59. Mated moths with spermatophores and nonmated moths falling in three fat-body classifications.

Class of fat body	Number of spermatophores					Total females		Males
	1	2	3	4	5	Mated	Nonmated	
1	4					4	11	20
2	1	2		1		4	132	107
3	11	3	8	5	1	28	60	137
Total	16	5	8	6	1	36	203	264
	44%	56%				15%	85%	52.4%

Table 3.—Summary of the morphological reproductive characteristics of three Noctuidae species.

Characteristic	*Heliothis zea*[a]	*Peridroma margaritosa*	*Pseudaletia unipuncta*
Aedeagus	Long; no caecum	Short; caecum	Short; caecum
Method of locking in bursa	Endophallic caeca	Aedeagal carina	Complexity of endophallus
Endophallus	Simple	Simple	Bifurcate
Cornuti	Present (simple)	None	Present (complex)
Bursa copulatrix	Membranous	Membranous	Heavily sclerotized
Cervix bursae	Twisted; contains all spermatophore collum	Saclike; contains part of collum in loop	Tip saclike; contains part of collum
Corpus bursae	Small; contains only spermatophore corpus	Large; contains corpus and part of collum	Large; contains corpus and part of collum
Spermatophore	Resilient, light	Springlike, heavy	Resilient, light
Frenum	Spinelike	Short "hooklike"	Lateral "shoe-horn"
Collum	Length of cervix	Looped in cervix	Length of cervix
Method of insertion in bursa	Endophallus in cervix only	Endophallus first in corpus, then cervix	Endophallus first in corpus, then cervix
Male scent gland	Scapal	Abdominal brush	Abdominal brush

[a]Callahan (1958b).

DISCUSSION AND SUMMARY

There is some evidence within this study of intraspecific variability, that is that certain specimens are more likely to complete successfully the mechanics of copulation than are other specimens. Out of 35 observed copulations of the earworm, one (2.8%) aberration (see photomicrograph,

Table 4.—Summary of functional reproductive characteristics of three Noctuidae species.

Characteristic	*Heliothis zea*[a]	*Peridroma margaritosa*	*Pseudaletia unipuncta*
Length of life	Short (7 days)	Medium (9 days)	Long (11 days)
Preoviposition period	2 nights	3 nights	3 nights[d]
Oviposition period	5 nights	6 nights	8 nights
Oviposition potential[b]	270×5=1,350	350×6=2,111[c]	290×8=2,320
Trapped females examined	1,753	239	1,611
Percentage of mating	56.9	15	Total sample 40.6 Baton Rouge 56.3
Range of samples	36.1–74.5	0–81	0–97.4
% single matings	58.6	45.5	44
% multiple matings	41.4	54.5	56
% of aberration	1/35=2.8	0/25=0.0	9/60=15.0
Sex ratios of ♂ to ♀	53 to 47	52.4 to 47.6	48.2 to 51.8
Oviposition dependent on mechanical stimuli	Yes	Yes	Yes[d]
Attracted plant fruit	Not necessarily	No	No
Baton Rouge seasonal curve	Buildup through summer	Spring and fall	Spring and fall

[a]Callahan (1958a, 1958b).
[b]These are theoretical potentials, based on mature egg counts times number of nights in the oviposition period.
[c]Walkden (1950).
[d]Breeland (1958).

Callahan 1958b) occurred (table 4). The male specimen expanded the endophallus into the small lateral corpus bursae first and it became so entangled with the emerging spermatophore that he was unable to separate after the normal time and died 2 days later, still attached to the female. This aberration illustrates the importance of the proper sequence and method of insertion during copulation (table 3). In 25 observed copulations of the variegated cutworm no aberration occurred; conversely, in 60 observed copulations (table 4) of the armyworm, 9 aberrations (15%) occurred. There seems to be evidence here that the more complex the method of insertion, the greater the instability. The method in the cutworm consists of feeding a rigid, springlike heavy collum first straight up into the corpus, then expanding the tip and feeding the remainder of the collum into the cervix. The spermatophores of both the earworm and armyworm are pliable, resilient, and light, and require much more manipulation than that of the cutworm. In this degree of hardness of the spermatophores the chemistry of spermatophore formation plays a part and is seen to vary between species. It appears that the more springlike and rigid the emerging spermatophore, the less the complexity of endophallus and cornuti. Examination of the fall armyworm, *Laphygma frugiperda*, also bears this out as it feeds a springlike spermatophore into the female bursa, and also has a short and simple endophallus. Obviously, species having a simple endophallus and springlike rigid spermatophore would not be able to copulate with the opposite-type species, and the need for an aedeagal locking device, as in *P. margaritosa*, is evident.

From the foregoing discussion it would seem that in any large population, although intraspecific variability does occur in regard to the mechanics of spermatophore formation, the percentages are so low they would not, to any great degree, affect the total percentage of mating in the population. In this respect spatial separation and attractibility of the sexes probably plays a far more important role.

Table 3 gives a concise summary of the morphological reproductive characteristics of the three species. A comparison of these noctuids indicates that at a subfamily level there is considerable variation in the mechanics of spermatophore insertion.

Table 4 is a summary of the functional reproductive characteristics of the three species. There is some evidence, both from the authors' egg counts and counts of others (Walkden 1950), that the longer lived species have a slightly higher egg potential. The range given by various workers is so great, however, that it is hard to say whether or not these differences contribute much to a greater potential economic destructiveness of the moths. The shorter lived moth seems to have a shorter preoviposition period. However, this is also subject to great variation, as the preoviposition period depends entirely on the time of mating. Eggs of these species are not deposited until after copulation and so the preoviposition period given (table 4) is the absolute minimum as no copulations have ever been observed prior to these times.

Once mated, oviposition in all three species will take place regardless of outside factors. It is important to note, however, that mechanical

stimulus of the ovipositor by surface texture is extremely important in all these species. This has been true of *P. margaritosa* in all cage experiments, where eggs were always deposited in batches on villous cloth. It has been proved for a certainty in the earworm (Callahan 1957a, 1957b) and in the armyworm (Breeland 1958). The ovipositor of each species is modified for the special requirements of egg deposition, and the reader is referred to Callahan (1958a) and Breeland (1958) for detailed descriptions of oviposition in the earworm and armyworm, respectively. Oviposition of *P. margaritosa* is quite similar to that of the earworm, with the exception that the moths remain stationary and deposit eggs in batches, rather than scattering single eggs while continually moving about.

The initial spatial separation of feral populations is, of course, unknown. We may only state that in cages *P. margaritosa* and *P. unipuncta* attain a much higher percentage of mating than *H. zea*. As pointed out previously, this may be due to the efficiency of the male releaser scent glands.

In the field the host plants, and not necessarily the fruiting parts, contribute to delineate the spatial separation of certain populations. Since in cages the male of all three species is attracted to the female we must assume the same of the field (Callahan 1958a and unpublished data). If we consider a static (nonmigratory) armyworm population, we reach the conclusion that the efficiency of the female attractability of this insect is at least equal to that of the earworm. If we consider the single Shreveport sample, this is probably also true of *P. margaritosa*. We are unable to determine the reason for the low degree of mating for the Baton Rouge population of the latter insect unless, as in the armyworm, we happened to trap a migratory population. In Baton Rouge the variegated cutworm and armyworm have a similar seasonal history (table 4), disappearing almost completely during midsummer.

In summarizing the reproductive pattern of these insects we find the armyworm to be long-lived, to have the most complicated reproductive pattern, and to be most variable in percentage of field mating, possibly due to mass movements. It attains a high degree of mating in cages but also has a much higher percentage of aberrations during copulation. The variegated cutworm is medium-lived, has a more simple reproductive pattern, a variable percentage of field mating (reason unknown), but a high degree of mating in cages and a very low percentage of aberrations during copulation. The short-lived earworm is considered to be of medium complexity in its reproductive pattern, and to have a low percentage of cage mating but a very stable percentage of mating in the field. Aberrations occur, but the percentage is quite low. All three species are considered to have accumulated functional and reproductive morphological differences to the degree that there exists between them a definite mechanical "lock-and-key" barrier that prevents crossing.

REFERENCES CITED

Breeland, S. G. 1958. Biological studies on the armyworm *Pseudaletia unipuncta* (Haworth) in Tennessee (Lepidoptera: Noctuidae). Jour. Tennessee Acad. Sci. 33: 263–347.

Callahan, P. S. 1957a. Oviposition response of the corn earworm to differences in surface texture. Jour. Kansas Ent. Soc. 30: 59–63.

1957b. Oviposition response of the imago of the corn earworm, *Heliothis zea* (Boddie), to various wave lengths of light. Ann. Ent. Soc. America 50: 444–52.

1958a. Behavior of the imago of the corn earworm, *Heliothis zea* (Boddie), with special reference to emergence and reproduction. Ann. Ent. Soc. America 51: 271–83.

1958b. Serial morphology as a technique for determination of reproductive patterns in the corn earworm, *Heliothis zea* (Boddie). Ibid. 413–28.

Cholodkovsky, N. 1884. Über die Hoden der Lepidopteren. Zool. Anz. 7: 564–8.

Davey, K. G. 1958. The migration of spermatozoa in the female of *Rhodnius prolixus* Stål. Jour. Exptl. Biol. 35(3): 694–701.

Ditman, L. P., and **E. N. Corey.** 1933. The response of corn earworm moths to various sugar solutions. Jour. Econ. Ent. 26: 109–15.

Forbes, W. T. M. 1939. The muscles of the lepidopterous male genitalia. Ann. Ent. Soc. America 32: 1–10.

Franclemont, J. G. 1951. The species of the *Leucania unipuncta* group, with a discussion of the generic names for the various segregates of *Leucania* in North America. Proc. Ent. Soc. Washington 53(2): 57–85.

Khalifa, A. 1950. Spermatophore production in *Galleria mellonella* L. (Lepidoptera). Proc. Roy. Ent. Soc. London (A) 25: 33–42.

Kusnezov, N. J. 1915. Faune de la Russie. Insectes Lépidoptères, Vol. 1, Liur. 1. 336 pp., 204 figs.

Mayr, E. 1942. Systematics and the Origin of Species. New York: Columbia University Press. 334 pp.

Musgreave, A. J. 1937. Histology of the male and female reproductive organs of *Ephestia kühniella*. Proc. Zool. Soc. London (B) 107: 337–64, 24 figs.

Norris, Maud J. 1932. Contributions towards the study of insect fertility. I. The structure and operation of the reproductive organs of the genera *Ephestia* and *Plodia* (Lepidoptera, Phycitidae). Proc. Zool. Soc. London 1932: 595–611, 5 pls.

Stitz, H. 1901. Der Genitalapparat der Mikrolepidopteren. 1. Der männlichen Genitalapparat. Zool. Jahrb., Abt. Anat. 14: 135–76, 5 pls.

Tracey, M. V. 1955. Chitin. *In*: K. Paech and M. V. Tracey (eds.), Moderne Methoden der Pflanzenanalyse. Berlin: Springer-Verlag.

Wadley, F. M. 1921. Life history of the variegated cutworm. Jour. Econ. Ent. 14: 272–7.

Weidner, H. 1934. Beiträge zur Morphologie und Physiologie des Genitalapparates der weiblichen Lepidopteren. Zeitschr. angew. Ent. 21: 239–90.

Williams, J. L. 1948. Anatomie comparée des genitalia internes de quatre espèces représentant quatre genres et deux sous-familles de Noctuidae (Lepidoptera). Rev. Franç. Lépidoptérologie 11: 238–50.

Zelensky, V. 1938. Contribution à l'étude de *Rhyacia saucia* Hbn. (Lepid. Noct.). Rev. Zool. Agric. 37(7–8): 103–12, 120–2, 1 fig.

A SYSTEMATIC STUDY ON THE STRAWBERRY APHID COMPLEX (PENTATRICHOPUS SPP.)[1]

G. A. SCHAEFERS[2]
New York State Agricultural Experiment Station, Geneva

ABSTRACT

The four species important as strawberry-virus vectors in North America are compared on the bases of abdominal chaetotaxy, distribution, and hosts. Due to inter- and intraclonal variation in the abdominal chaetotaxy, species frequently are difficult to distinguish unless large samples are examined. *P. fragaefolii* (Ckll.) and *P. thomasi* H.R.L. are widely distributed in the United States, the former being more rare in the Southeast; both of these species colonize strawberry, rose, and *Potentilla*. *P.* **jacobi** (*P. thomasi jacobi* H.R.L.), occurring only on certain wild *Fragaria* species in the Western United States, is raised to specific status. *P. minor* (Forbes) (=*P. brevipilosus* (Baerg), suggested new synonymy), found in the Eastern United States, has not been collected from rose or from *Potentilla*. A pronounced morphological variant of *P. minor* is noted; apterous males and oviparae of *P. thomasi* are described; a redescription of viviparae and a tentative description of oviparae of *P. jacobi* are provided; and a first report of apterous males of *P. fragaefolii* in North America is included. Of the other two North American *Pentatrichopus* species, *P. potentillae* (Walker) has not been found to carry strawberry virus, while *P. tetrahodus* (Walker), though a vector, is of minor importance because of its restriction to rose as a host.

Within the last three decades, five species of the genus *Pentatrichopus* have been found to be vectors of strawberry viruses. Of these, *P. fragaefolii* (Cockerell), *P. thomasi* (Hille Ris Lambers), and *P. minor* (Forbes) are known to be of major importance. *P. jacobi* (Hille Ris Lambers), due to its limited distribution, and *P. tetrahodus* (Walker), because it is restricted to rose as a host plant, are of minor importance as virus vectors. *P. potentillae* (Walker), the sixth member of the genus in North America, occurs only on *Potentilla* spp. and has not been incriminated as a strawberry virus vector. Until a recent publication by Hille Ris Lambers (1953), considerable confusion existed in the systematics of this group.

Because the group is so important, and because of the amount of morphological variation it displays in North America, further investigation of the various morphotypes, morphological variations, distributions, and host ranges of the species involved has become essential. Of the three major species in North America, only *P. fragaefolii* is known to occur elsewhere in the world. But in the United States and Canada the presence of several very similar species has resulted in much difficulty. The present paper aims toward clarification of this species complex as far as possible.

Hille Ris Lambers (1953) characterized the genus *Pentatrichopus* Börner by the presence of long, capitate hairs on the body and five hairs on the first tarsal joints of the adult. As it differs from the genus *Chaetosiphon* Mordvilko only in lacking capitate hairs on the siphunculi, he classified *Pentatrichopus* as subgeneric to *Chaetosiphon*.

The abdominal chaetotaxy is the main character used for distinguishing the species within the genus. *P. thomasi* (fig. 1) shows this chaetotaxy in its fullest complement, with eight longitudinal rows of setae present on the first four abdominal tergites. These consist of two dorsal rows (often with two setae per nodule), two pleural rows, two submarginal rows, and two marginal rows. Among the species occurring on strawberry there is a successive loss of various setae (fig. 2). This will be the characteristic primarily used in discussing the morphological variation among the members of the group.

Pentatrichopus fragaefolii (Cockerell)

Myzus fragaefolii Cockerell, 1901, Canadian Ent. 33(4): 101 (alate and apterous viviparae on cultivated strawberry, Jerome, Arizona); lectotype, U. S. Natl. Mus., Slide 9337. Davidson, 1914, Jour. Econ. Ent. 7(1): 127–36 (oviparous female and alate male; host not clear).

Myzus fragariae Theobald, 1912, Entomologist 45(591): 223–4 (alate and apterous viviparae; cultivated strawberry, England).

Capitophorus fragariae, Theobald, 1926, Aphidae of Great Britain 1: 244–6. Hodson, 1937, Bull. Ent. Res. 28(3): 409–16, in part.

Capitophorus fragaefolii, Hottes and Frison, 1931, Bull. Illinois Nat. Hist. Surv. 19(3): 283. Balachowsky and Mesnil, 1935, Ins. nuisibles aux plantes cultiv. 1: 440. Palmer, 1952, Aphids of Rocky Mountain Region 256–7.

Pentatrichopus fragaefolii, Börner and Schilder, 1932, in Sorauer's Handbuch der Pflanzenkrankh. 5: 619.

Pentatrichopus potentillae (Walker), Hille Ris Lambers, 1933, Stylops 2(8): 169–76. Massee, 1935, Rept. East Malling Res. Sta. No. 22: 173–6.

Capitophorus potentillae, Harmson, 1934, Tijdschr. Plantenziekten 49(6): 137–52 (oviparae; Europe).

Pentatrichopus fragariae, Thomas and Jacob, 1941, Proc. Roy. Ent. Soc. London (B) 10(6–7): 107–23, in part.

Passerinia fragaefolii, Börner, 1952, Mitteil. Thüringische Bot. Ges. 4: 118, 252.

Chaetosiphon (Pentatrichopus) fragaefolii, Hille Ris Lambers, 1953, Temminckia 9: 65–74, in part.

[1]Journal paper No. 1202, New York State Agricultural Experiment Station, Geneva, December 18, 1959. Accepted for publication March 25, 1960.

[2]The author wishes to acknowledge with thanks the aid and guidance provided by Dr. W. W. Allen during much of the research. Appreciation is expressed to E. O. Essig, to D. Hille Ris Lambers, and to Miss Louise M. Russell for their suggestions and opinions concerning the subjective elements in the problem. Thanks are extended also to Dr. P. J. Chapman for his kind assistance in reviewing this manuscript.

Hodson (1937) disputed the synonymy of *P. fragaefolii* (Cockerell) and *P. fragariae* (Theobald) which earlier was proposed by Hottes and Frison (1931). He concluded that the viviparous forms in England corresponded to those described by Theobald (1912) as *Myzus fragariae* and that, although almost indistinguishable morphologically, they were of a species distinct from the American *fragaefolii*. His opinion, however, was based primarily on the marked differences he observed between the sexual forms attributed to *P. fragaefolii* by Davidson (1914) and the sexual forms of "*P. fragariae*" in Europe.

Thomas and Jacob (1941), who examined material collected in the United States and Canada, concluded that possibly two species of strawberry aphids occurred in North America. One of these was indistinguishable from the European *P. fragariae* (Theobald). They noted

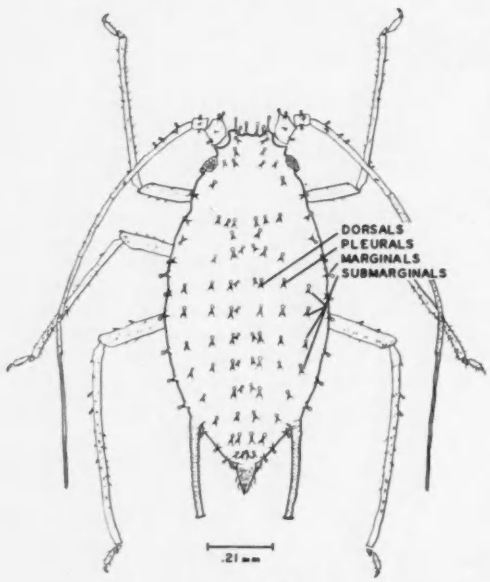


FIG. 1.—Abdominal chaetotaxy of *Pentatrichopus thomasi* (H.R.L.).

the existance of a light form and a dark form of the second one, which was distinct from both *P. fragariae* and *P. potentillae* (Walker). The synonymy of *P. fragariae* and *P. fragaefolii* depended, therefore, upon which of the two species seen by Thomas and Jacob was the one Cockerell had described as *fragaefolii*.

Hille Ris Lambers (1953) reported that examination of Cockrell's types showed them to conform to the European species previously described as *P. fragariae* (Theobald). As the name *P. fragaefolii* had priority, *P. fragariae* was placed in synonymy. Hille Ris Lambers described the second species of Thomas and Jacob (1941) as *P. thomasi*, and designated the dark form distinguished by them as *P. thomasi jacobi*.

All forms of *P. fragaefolii* were well described by Hille Ris Lambers (1953). He noted that the chaetotaxy of this species may, in some cases, be indistinguishable from that of *P. thomasi*—i. e., some morphological overlap occurs. In describing *P. fragaefolii* he stated, "Very rarely IIIrd and/or IVth tergite with one or more pairs of hairs placed between pleural and normal marginal hairs"; and of *P. thomasi* he said, "In exceptional specimens the inner pair of marginal hairs is absent on most of the mentioned segments."

In order to determine the amount of variation in the abdominal chaetotaxy of *P. fragaefolii*, collections were made and the numbers of setae in the submarginal rows were tabulated. The disparity in these rows is most completely expressed by the presence in *P. thomasi* of eight submarginal setae, four in each row (fig. 2), and by the total absence of such setae in *P. fragaefolii*. Gain or loss of setae appears to occur at random at any one of the eight positions. Each aphid, therefore, could be classified according to the total number of setae (from zero to eight) present in the submarginal rows. Frequency polygons were then constructed, showing the percentage of aphids in the sample populations that occurred in each numerical setal classification.

Figure 3 shows the setal-class frequencies of a greenhouse population reared at Berkeley, California. Setal classes in this population ranged from zero to six setae (mean, 1.1 per aphid). Approximately 59% of the aphids in this sample had gained additional setae, but the absence of the seven- and eight-setal classes indicated that only *P. fragaefolii* was present.

Figure 4 shows the setal-class distribution in a sympatric population of *P. fragaefolii* and *P. thomasi* at Santa Clara, California. This exhibits a bimodal setal-class frequency, with aphids represented in all setal classes from zero to eight. Those with the full complement of eight setae in the submarginal rows made up 20% of the total sample, and 56% of the sample possessed no additional setae in the submarginal rows.

In order to determine the affinities of the intermediate classes in the Santa Clara population, laboratory rearings were conducted. To provide confidence in selecting the correct species for parents, only aphids with one seta or none (*P. fragaefolii*) and others with seven or eight (*P. thomasi*) were used. Since the numbers of setae present on the offspring are not restricted precisely to those of the parents, it was felt that the variation in number of setae between parents and offspring would be representative of the variation in the population as a whole.

The results showed the progeny of *P. fragae-*

folii to be extremely homogeneous, with setal classes ranging only from zero to one, as in the parents, and with more than 95% of the offspring falling in the zero class (fig. 5). Variation among the progeny from *P. thomasi* accounted for the rest of the distribution, and even for a very small percentage of those in the one-setal class (fig. 6). The range of variation in the Santa Clara population of *P. fragaefolii*, as seen in these results, was markedly different from the zero-to-six range of setae exhibited by the Berkeley greenhouse population. However, since both possessed modal classes of zero setae, by definition they were *P. fragaefolii*.[4]

Several collections of *P. fragaefolii* made in New York show setal-class frequencies very similar to those of the Santa Clara clone. Hille Ris Lambers (1958) has found the chaetotaxy of this species in Europe surprisingly uniform; and from his description quoted above, the occurrence of additional setae in the submarginal rows appears to be rather rare. Examination of numerous European specimens by the author has confirmed this. In view of the interclonal variation observed in North America, apparently *P. fragaefolii* in Europe represents the introduction of a single, rather uniform clone. This would account for the slight variability attributed to this species by Hille Ris Lambers (1953). The variation in the species as a whole is considerably greater. In North America it has resulted in a lessened degree of morphological distinction between *P. fragaefolii* and *P. thomasi*.

Sexual Forms.—Since only *P. fragaefolii* occurs in Europe, Hodson's (1937) description of the sexuales can be accepted as properly associated with that species. Davidson (1914) earlier had described sexual forms in North America which he attributed to *fragaefolii*, but Hodson found that Davidson's description did not fit the European oviparae, which lacked the prominent group of noncapitate hairs beneath the cauda and whose caudae were not dusky. A recent collection made at Grass Valley, California, has shown that oviparae of *P. thomasi* possess these characters that Davidson ascribed to *fragaefolii*.

Although he recognized the possibility that a single species may have both alate and apterous males, Hodson pointed out that the males described by Davidson were alate while those of European *fragaefolii* were apterous. Hille Ris Lambers (1953) remarked that this did not necessarily prove that Davidson had dealt with *P. thomasi*, and reported that G. H. L. Dicker, of the East Malling Research Station, had reared both alate and apterous males from the same culture of *P. fragaefolii*.

Extensive collecting in California has shown that sexual forms of *P. fragaefolii* very rarely occur there, and that overwintering is accomplished almost entirely by viviparae. All oviparae collected were identical with those from Europe; and, in contrast with Davidson's findings, the males collected were apterous and conformed with European males. This finding, plus the caudal characteristics of the oviparae, suggested that Davidson's collection was, in fact, *P. thomasi*. However, males of *P. thomasi* collected subsequently in California also were apterous. Thus it is still uncertain which was the exact species referred to by Davidson (1914); and, as Davidson (1959) doubts that his slides still exist, probably this question will never be resolved. One possibility suggested by the similarities in the oviparae is that his was a collection of *P. thomasi*, and that this species only very

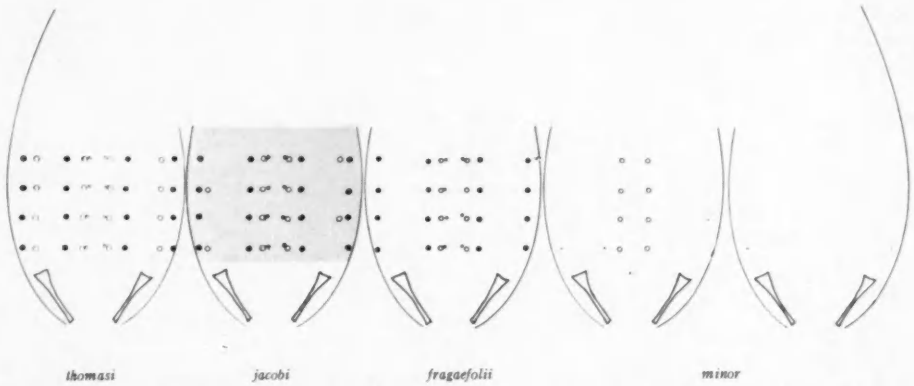


FIG. 2.—Comparative diagram illustrating the abdominal chaetotaxy in four species of *Pentatrichopus*.

[4]After this paper was submitted for publication, Frazier (1960) found the greenhouse population of *P. fragaefolii* to possess unique vector characteristics.

rarely produces alate males in the Western United States. However, his collection may possibly have consisted of *P. jacobi*, as he inferred that the sexuales came from a wild species of *Fragaria*.

In one season's collecting by the author in the Northeastern United States, the only sexuales taken belonged to a variant form of *P. minor*, and none were found of *P. fragaefolii*. In this area overwintering takes place almost exclusively in the egg stage, and it seems likely that *P. fragaefolii* and *P. thomasi* also conform to this pattern here. Hottes and Frison (1931) reported the occurrence of sexual forms of *P. fragaefolii* in Illinois, but did not mention whether the males were alate or apterous.

native American parent stock (Darrow 1937), quite possibly *P. fragaefolii* may have been transported to Europe either on the parent stock or on hybrid varieties.

This is the most widespread member of the complex, and is the only one known to occur throughout the world, wherever strawberries are grown. Hille Ris Lambers (1953) recorded its occurrence throughout Europe, Palestine, Eritrea, North America, Argentina, and New Zealand. In the United States it has been collected in California, Oregon, Washington, Idaho, Utah, and Arizona; and Russell (1958) has furnished records of it from Wisconsin, Massachusetts, New York, and Florida. In Canada it is known

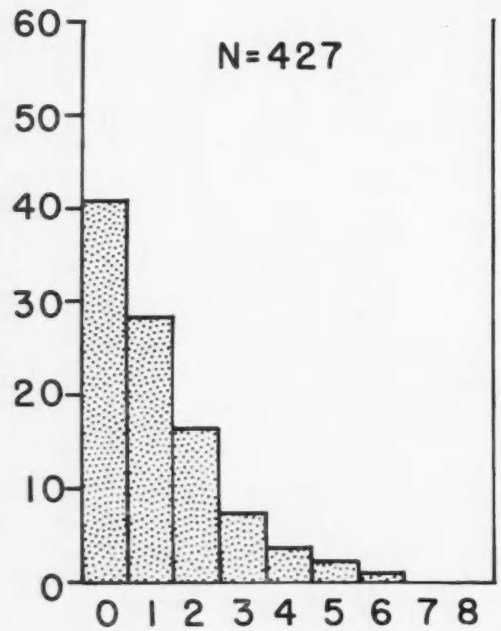


FIG. 3.—Occurrence of setae in submarginal rows of *P. fragaefolii* (Ckll.) from Berkeley, California.

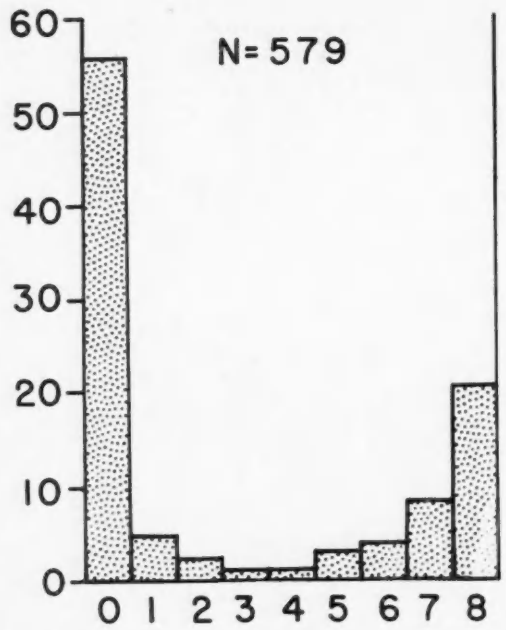


FIG. 4.—Occurrence of setae in submarginal rows of sympatric population, *P. fragaefolii* and *P. thomasi*, at Santa Clara, California.

Distribution.—Balachowsky and Mesnil (1935) were the first to suggest that the strawberry aphid *P. fragaefolii* is native to North America, basing their conclusion on the facts that it was originally described from the United States in 1901, yet was not reported in Europe until 1912. Hille Ris Lambers (1958) also holds the opinion that it was native to North America. Earlier (1953), he pointed out that prior to Theobald's (1912) description of *P. fragariae*, aphid students in Europe recorded and described strawberry-dwelling aphids that are now much rarer on that host plant than *P. fragaefolii*. Since commercial varieties of strawberry have been developed from

from British Columbia (Dicker 1956, Forbes 1959) and New Brunswick (MacGillivray 1959). Except for a single report from Florida, preliminary findings indicate its absence from the southeastern quadrant of the United States. Demaree and Marcus (1951) reported that apparently it was scarce east of the Mississippi River; and, though numerous collections had been made, this species was found only in New York and Wisconsin. On a local basis, *P. fragaefolii* often is found sympatrically with *P. thomasi* and/or *P. minor*, but frequently it occurs alone.

Hosts.—Dicker (1952) noted that in Europe *P.*

fragaefolii has no important natural host other than strawberry. Generally speaking, this is the case in North America also. However, in certain instances, various wild hosts do sustain considerable populations of this aphid, although they are not essential as alternate hosts.

Among the *Fragaria* species, the cultivated varieties of strawberry are the hosts on which this aphid most commonly occurs. Present information indicates that it does not readily infest the thin-leaved wild strawberries. However, Thomas and Jacob (1940) induced it to colonize on *F. moschata* Duch., and in Europe it has been found occasionally infesting *F. vesca* L., the common species of wild strawberry there (Massee et al. 1938, Dicker 1952). Though such occasions in nature apparently are rare, there are numerous reports that *F. vesca* may readily be infested artificially, or when this host is removed from its natural habitat (Massee 1935, Hodson 1937, Thomas and Jacob 1940, Greenslade 1941, Essig). Massee (1935) was able to induce it to live on *P. sterilis* Garcke. *Potentilla* is a widespread genus with a large number of species, and the paucity of aphid material from them indicates that they are not very favorable hosts for the strawberry aphid.

Hodson (1937) induced *P. fragaefolii* to breed on *Rosa*. Thomas and Jacob (1940) found it infesting cultivated roses on one occasion; and the author has observed this several times in California. Miller and Darrow (1954) reported the singular collection of this aphid on wild roses in Oregon.

Pentatrichopus thomasi (Hille Ris Lambers)

Chaetosiphon (*Pentatrichopus*) *thomasi* Hille Ris Lambers, 1953, Temminckia 9: 65–74 (in part) (North America; type specimens in collection of H.R.L.; apterous and alate viviparae).

This species was first referred to by Thomas and Jacob (1941), and the viviparous forms were

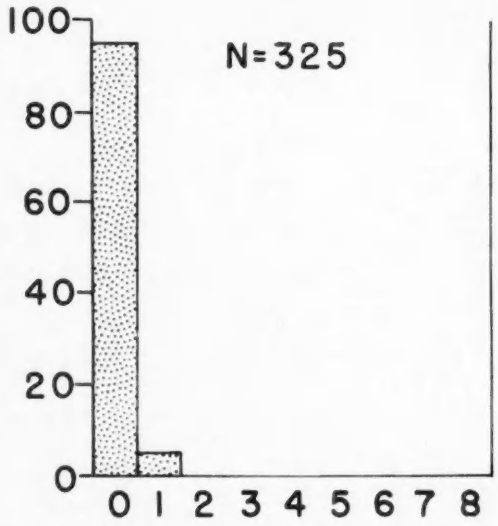


FIG. 5.—Occurrence of setae in submarginal rows of offspring from parents with one or no setae.

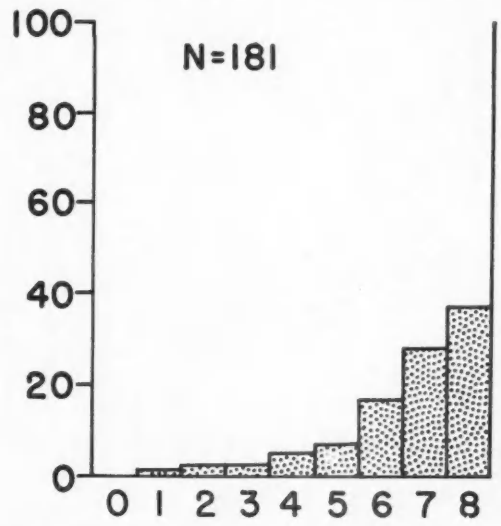


FIG. 6.—Occurrence of setae in submarginal rows of offspring from parents with seven or eight setae.

Hille Ris Lambers 1953). In North America *P. fragaefolii* has been collected on the thick-leaved beach strawberry, *F. chiloensis* L., both under natural conditions and under cultivation. This host species, native to the West Coast of the Americas, was one of the original parents from which all cultivated varieties of strawberry were derived (Darrow 1937).

Pentatrichopus fragaefolii has been reported to occur on *Potentilla anserina* L. (Massee et al. 1938) and on *P. comarum* Nestl. (Whitehead and Wood 1946), and it has been collected on *P. douglassi* Greene (slide in collection of E. O. subsequently described by Hille Ris Lambers (1953). The principal character distinguishing it from *P. fragaefolii* is the presence of the submarginal rows of setae (fig. 1). As noted above Hille Ris Lambers stated that exceptional specimens lacked the inner pairs of marginal setae on most of the mentioned segments. Using methods like those described under *P. fragaefolii*, populations of *P. thomasi* were sampled and analyzed for setal-class frequencies.

In contrast to the frequency distributions shown by *P. fragaefolii* (figs. 3, 5), the population of *P. thomasi* from Grass Valley, California, exhibited

a single mode of eight setae in the submarginal rows (fig. 7), with a setal-class range from one to eight (mean, 7.0) per aphid. Although 58% of the aphids examined lacked one or more setae in the submarginal rows, the absence of a modal class of zero setae indicated that only *P. thomasi* was present. When parents with seven to eight setae, from the Santa Clara population, were bred, their offspring provided a distribution of setal classes like that occurring naturally in the field, overlapping *P. fragaefolii* only in the one-setal class.

Sexual Forms.—These forms, which have not previously been reported or described, were collected at Grass Valley, California, on cultivated strawberry. There was little doubt of their identity, as they were collected from colonies of viviparae which, on the basis of their setal counts (fig. 7), were shown to consist only of *P. thomasi*. Sexuales, together with large numbers of eggs, were collected from this area during two successive winters. Their descriptions follow.

Apterous Oviparous Females.—Living specimens shiny green when gravid, with five or six eggs showing through integument as paler spots, turning to dull green and finally to pale yellow with increasing age. Antennae (mounted specimens) not exceeding base of cornicles, segments 3 to 6, or at least 5 and 6, dusky; base of segment 3 with two or three prominent, capitate setae. Legs dusky, except coxae and trochanters; proximal two-thirds of tibiae swollen with 40 to 60 circular sensoria. Cauda often very dark, short-tapering, with several long, noncapitate setae on ventral plate. Additional setae in submarginal rows of abdominal tergites 1 to 4, as in viviparae. Measurements as in table 1.

Apterous Male.—Living specimens pale green to brown, with dusky transverse markings on dorsum, presenting an overall darkened appearance. Head of mounted specimens very dark, covered with small, noncontiguous nodules; antennae with all segments dark brown, rhinaria as in *P. fragaefolii*. Legs (except base of femora), cauda, and cornicles darkened. Body setae as in viviparae, with additional setae between pleural and marginal rows of abdomen, but a full complement of setae not present in any individual observed. Measurements as in table 1.

Distribution.—*Pentatrichopus thomasi* is only known to occur in North America. In the United States it has been collected in California, Oregon, Idaho, Utah, New York, and West Virginia; and Russell (1958) reported that she had slides also of specimens from Illinois, Maryland, Massachusetts, New Jersey, Ohio, Wisconsin, Tennessee, and Virginia. Demaree and Marcus (1951) noted the occurrence of "an unnamed species of *Capito-*

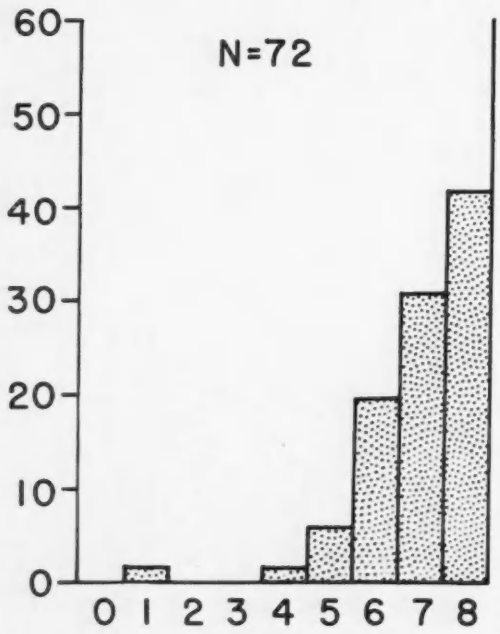


FIG. 7.—Occurrence of setae in submarginal rows of *P. thomasi* at Grass Valley, California.

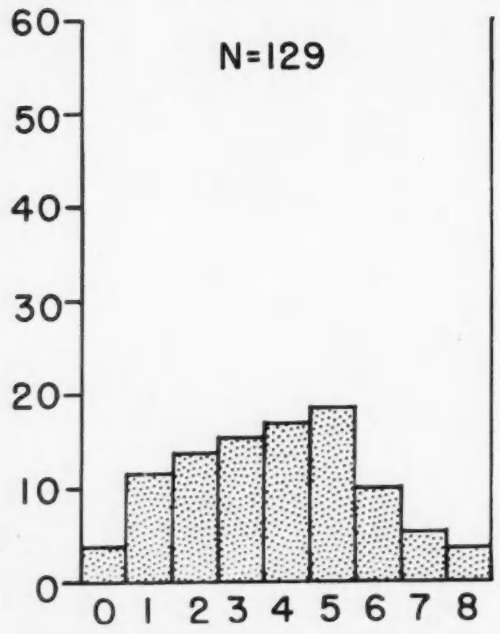


FIG. 8.—Occurrence of setae in submarginal rows of *P. jacobi* (H.R.L.) from Watsonville, California.

phorus" (presumably *P. thomasi*) from Delaware and North Carolina. In Canada it has been found in British Columbia (Forbes 1959) and in New Brunswick (MacGillivray 1959). This species thus appears to be widespread, occurring throughout northern North America, at least, wherever strawberries are grown. Of possible significance in its known distribution is its absence from the Southeastern United States, including the three States bordering the southern part of the Mississippi River.

Hosts.—*P. thomasi* commonly occurs on cultivated strawberries. Thus far it has not been taken on the thin-leaved wild strawberries, but it has been found on the beach strawberry, *Fragaria chiloensis*, in California. Thomas and Jacob (1941) reported the collection of a strawberry aphid different from *P. fragaefolii* on wild strawberry, but it is not clear whether they were referring to *P. thomasi* or *P. jacobi*.

Pentatrichopus jacobi (H.R.L.), new status

Chaetosiphon (*Pentatrichopus*) *thomasi jacobi* Hille Ris Lambers, 1953, Temminckia 9: 65–74 (North America; apterous and alate viviparae; types in collection of H.R.L.).

This species was first referred to by Thomas and Jacob (1941), who observed two species of strawberry aphids in North America, one of which differed from *P. fragaefolii* (*fragariae* Theob.) and which occurred in both a dark and a light form. When he described the light form as *P. thomasi*, Hille Ris Lambers regarded the dark one as a variety and named it *P. thomasi jacobi*. Recent investigations, utilizing larger samples, show that this "dark form" is more distinct, both morphologically and biologically, than was previously suspected, so that it merits specific recognition. Descriptions of viviparae and oviparae follow.

Apterous Viviparae.—Like *P. fragaefolii*, but differing in the expression of much darkening of the terga as an adult. Additional capitate setae present in submarginal rows of abdominal tergites 1 to 4, the average number of such additional setae, however, intermediate between those of *P. fragaefolii* and *P. thomasi*. Measurements as in table 2.

Table 1.—Measurements of 10 apterous oviparous females and 10 males of *Pentatrichopus thomasi* (*H.R.L.*).

	Females		Males	
	Range	Mean	Range	Mean
	mm.	*mm.*	*mm.*	*mm.*
Length of body[a]	1.300–1.470	1.390	0.90 –1.03	0.97
Length of cornicle	0.285–0.335	0.313	0.18 –0.22	0.20
Hind femur	0.325–0.415	0.368	0.26 –0.32	0.29
Hind tibia	0.525–0.665	0.588	———	———
Cauda	0.105–0.115	0.112	0.065–0.075	0.07
Antennal segment 1	0.045–0.075	0.057	———	0.06
2	0.045–0.055	0.048	———	0.05
3	0.245–0.275	0.259	0.29 –0.32	0.30
4	0.150–0.200	0.169	0.18 –0.22	0.19
5	0.205–0.230	0.214	0.20 –0.23	0.21
6	0.420–0.490	0.466	0.43 –0.53	0.48

[a]From vertex to tip of cauda.

Alate Viviparae.—Like *P. fragaefolii*, differing primarily in antennal characteristics. In the nine specimens observed, segment 5 was always longer than segment 4; rhinaria 16 to 20 (generally 18 to 20) on segment 3, 0 or 1 (rarely 2) on segment 4, none observed on segment 5. Measurements as in table 2.

Oviparae.—This tentative description is based on the single specimen collected. Generally like *P. fragaefolii*, differing by the presence of somewhat darkened transverse bands on the pro- and mesothoracic tergites. Antennae with only a few, blunt, minute setae; antennae slightly

Species of *Pentatrichopus* have not been observed by the author on any of the various species of *Potentilla*, but Thomas and Jacob (1941) collected a species "different from *P. fragaefolii*" on such a host. Their species may have been *P. thomasi*, as two slides in the collection of E. O. Essig indicate that this aphid does occur on at least two species of *Potentilla*, namely *P. anserina* L. and *P. gracilis nigida* Dougl.

On numerous occasions small populations of this aphid were collected on cultivated roses in California during the fall and winter; and once, in Oregon, a wild *Rosa* was found heavily infested with *P. thomasi* in July. Miller and Darrow (1954) reported collecting a "*Capitophorus* sp. near *fragaefolii*" from wild rose at six different locations in Oregon.

The host ranges of *P. thomasi* and *P. fragaefolii* seem not to differ, except for the more frequent occurrence of the former on wild *Rosa*.

Table 2.—Measurements of 10 apterous and 9 alate viviparae of *Pentatrichopus jacobi* (H.R.L.)

	Apterous			Alate		
	Range (mm.)	Mean (mm.)	Ratio to Ant. 3	Range (mm.)	Mean (mm.)	Ratio to Ant. 3
Cornicle	0.30–0.37	0.32	1.01	0.23–0.30	0.25	0.66
Hind femur	0.29–0.36	0.32	0.98	0.34–0.42	0.37	0.98
Hind tibia	0.55–0.70	0.61	1.93	0.74–0.87	0.78	2.06
Antennal 3	0.29–0.37	0.32	1.00	0.34–0.46	0.38	1.00
4	0.14–0.23	0.19	0.59	0.20–0.24	0.22	0.57
5	0.17–0.24	0.20	0.63	0.22–0.28	0.24	0.64
6	0.54–0.60	0.55	1.72	0.56–0.67	0.60	1.59

exceeding length of body. Abdominal chaetotaxy as in viviparae, with three additional setae occurring in submarginal rows of first four abdominal tergites. Setae beneath the cauda short, noncapitate. Measurements: body length 1.46 mm.; cornicle 0.33 mm.; hind femur 0.36 mm.; hind tibiae 0.66 mm.; antennal segments 1 to 6, respectively, 0.06, 0.06, 0.35, 0.21, 0.22, and 0.56 mm.

No males of this species have been found.

According to Hille Ris Lambers (1953), the principal difference between *P. fragaefolii* and *P. thomasi* is the presence of two rows of marginal setae on the anterior abdominal tergites of the former, and of four such rows on the latter. This character is particularly valuable when comparing *P. thomasi* with certain clones of *P. fragaefolii*, such as that in Europe where additional setae occur very rarely. On the basis of this character *P. jacobi*, possessing some additional setae, appears much more closely related to *P. thomasi* than to *P. fragaefolii*.

When larger samples of *P. jacobi* were studied, the frequency with which additional setae occurred in the submarginal rows was found to be intermediate between those of *P. fragaefolii* and *P. thomasi* (fig. 8). This population was quite variable, with the additional setae of various individuals covering the entire range from zero (typical of *fragaefolii*) to eight (typical of *thomasi*). However, these two extremes showed the lowest frequencies of all, and the mode for the sample population was five additional setae.

The darkening of the terga in the viviparae has proved to be a valid character. It recurred through several generations when this species was reared under experimental conditions that differed markedly from those in the field. At various times of the year, particularly during cool weather, individuals of both *P. fragaefolii* and *P. thomasi* might be found with terga somewhat darkened, but this never reached the degree of darkening expressed by *P. jacobi*. This melanization was not apparent in the nymphs or in the young adults.

In addition to the distinguishing characters found in the apterous viviparae, others occur in the alatae and oviparae. The number of rhinaria on antennal segment 4 is of particular value.

Biological differences also mark *P. jacobi* as a distinct entity. To date, it has been found only on the thin-leaved wild *Fragaria* species, particularly *F. californica* C. and S. It has not been collected from the heavy-leaved *F. chiloensis*, or on cultivated strawberries, or on *Rosa* or *Potentilla*. Under laboratory conditions, however, it can be reared on most *Fragaria* species. Its distribution apparently is limited to the Western United States.

Pentatrichopus minor (Forbes)

Siphonophora minor Forbes, 1884, 13 Rept. State Ent. Illinois, 98–104 (North America; Slide 3158 in Illinois Nat. Hist. Surv. collection; apterous and alate viviparae).

Myzus minor (Forbes), Davis, 1911, Jour. Econ. Ent. 4(3): 325–31.

Myzus brevipilosus Baerg, 1922, Arkansas Agric. Expt. Sta. Bull. 179: 1–16. NEW SYNONYMY.

Capitophorus minor (Forbes), Hottes and Frison, 1931, Bull. Illinois Nat. Hist. Surv. 19(3): 284–5 (orig. descr. alate male, slide 8408, and oviparae, slide 8407, Illinois Nat. Hist. Surv. collection). Gillette and Palmer, 1934, Ann. Ent. Soc. America 27(2): 152.

Chaetosiphon (Pentatrichopus) brevipilosus (Baerg), Hille Ris Lambers, 1953, Temminckia 9: 132–74.

Chaetosiphon (Pentatrichopus) minor (Forbes), Hille Ris Lambers, 1953, loc. cit.

This species was originally described from Illinois by Forbes (1884), who stated, "All about the head and on the terminal segments of the abdomen are scattered a few stout, short, capitate hairs, which in the young are likewise distributed over the back."

Apparently unaware of Forbes' report, Baerg (1922) described and named *Myzus brevipilosus* from Arkansas, comparing it with *fragaefolii* and stating it to be markedly different. In referring to the distinguishing characters, he wrote, "Foremost among these are the capitate hairs, all over the body, which are long and very conspicuous in *Myzus fragaefolii* Ckll., whereas in *M. brevipilosus* n. sp. these hairs are considerably shorter

and found only on the head and on the last two segments of the abdomen." It is apparent from Baerg's description that *P. brevipilosus* is virtually identical with *P. minor*.

In discussing the three preceding species of *Pentatrichopus*, comparisons were possible on the basis of a discontinuous variable, i.e., the number of setae in the submarginal rows. In the *P. minor* group, however, there is greater variation in a continuous variable, namely, the size of the setae on the first four abdominal segments. Although the descriptions quoted above refer to the absence of capitate setae on the anterior abdominal segments, study of many specimens has shown that most of these setae are not absent but have become very minute.

Several collections from New York, as well as one from West Virginia, have revealed the presence of a form which was thought at first to represent a new species. Entire populations were noted to possess very prominent setae in the dorsal rows only, while single marginal rows were seen to be vestigial (fig. 2), and some individuals possessed only a few prominent setae in the dorsal rows. There seemed to be a complete gradation from those with prominent dorsals down to those with all setae extremely vestigial on the first four abdominal tergites—i.e., typical of *P. minor*. Although such gradation occurred, there was a definite tendency toward one variant or the other—with or without prominent dorsal setae.

When uniparental clones were reared, the offspring in all cases conformed generally with the parent. On rare occasions, however, an individual offspring of a parent with prominent dorsal setae exhibited vestigial setae. Similarly, some individual offspring from typical *P. minor* parents exhibited a few prominent dorsal setae. No such gradation has been observed between those with prominent dorsals and *P. fragaefolii*. These observations indicate that those with prominent dorsals are a variant of *P. minor*, and that this group is validly distinct from other members of the *Pentatrichopus* complex.

Sexual Forms.—Hottes and Frison (1931) described the oviparae and alate males of this species. Palmer (1952) reported that the measurements of alate males taken in copula with oviparae of *P. minor* agreed with the measurements given by Hottes and Frison (1931) for *P. fragaefolii*, and concluded that this threw some doubt on the distinctness of these two species.

The collection studied by Hotten and Frison was made in Illinois during October. Baerg (1922) reported that sexual forms had not yet been observed in the Ozark region, but thought that sexuales presumably occurred in New York. Alate males and oviparae of this species were found in a collection received by the author from West Virginia, likewise made during October; the oviparae correspond to the variant of *P. minor* possessing prominent dorsals. Several collections made in New York State during the past year have revealed that *P. minor* overwinters there almost exclusively in the egg stage; and, as in Illinois and West Virginia, males in the New York area are alate. They were collected there from September through December. Demaree and Marcus (1951)reported that *P. minor* overwinters in the egg stage in Maryland.

Distribution.—In the United States, *Pentatrichopus minor* is eastern in its distribution. The author has collected it in New York on several occasions. Russell (1958) has reported that slides of *P. minor* show its presence in Wisconsin, Michigan, Illinois, Ohio, Massachusetts, New Jersey, Maryland, Virginia, Kentucky, Missouri, Arkansas, Tennessee, North Carolina, Mississippi, and Louisiana. In Canada, MacGillivray (1959) noted that it ranges into New Brunswick, and Richards (1959) found it in British Columbia. This species thus appears to occur in all of the States east of the Mississippi River, in Missouri, Arkansas, and Louisiana, and in southern Canada.

Several collections from Arkansas show only the presence of typical *P. minor*, with all setae vestigial on the anterior abdominal segments. Fulton (1959) mentioned that several earlier collections from that State were all identified as *minor*. The author has seen specimens with prominent dorsals only from New York and West Virginia; and Russell (1958) observed that the aphids showing variation in the size of dorsal setae were all northern, except for two specimens from Tennessee. This distribution may represent an overlapping area between *P. fragaefolii* and *P. minor*.

Hosts.—To date, this species has been found only on species of *Fragaria*. Most reports pertain to cultivated strawberry only (Forbes 1884, Hottes and Frison 1931, Baerg 1922), and only Rorie (1957) has reported it as occurring on wild strawberry plants.

DISCUSSION

Four species of *Pentatrichopus* occurring in North America have strawberry as their major host. By using abdominal chaetotaxy, all four can be distinguished, at least on a population-wide basis. This study shows, however, that a certain amount of both intra- and intercolonal variation occurs within each species. Thus, offspring from a single parent may develop with different numbers of additional setae in the submarginal rows and elsewhere. Why variation should occur with parthenogenetic reproduction where only simple mitotic division takes place, is a moot question. The author assumes that epigenetic factors are involved, and that intraclonal variation which results may be compared to cellular differentiation during development—that is, differences in cytoplasmic materials may influence the final phenotype. Such a theory is not new to genetics. Another possibility, no

less remote, is an influence of genetic expression by supernumerary chromosomes. Preliminary investigations by Dr. Stanley G. Smith[3] indicate that such chromosomes may exist within this genus.

The problem of intraclonal variation may lead to further difficulties in separating the species presently recognized. Thus, different clones of the same species, particularly in *P. fragaefolli* and *P. minor*, exhibit different amounts of variation. Additional clones may possibly be found in the future which will bridge the "morphological gaps" now used to distinguish the species.

Except for the case of the *P. minor* with prominent dorsal setae, there seems to be no advantage in distinguishing between the interclonal variants, and to do so would undoubtedly lead to confusion. Until additional biological information is obtained to resolve the problem otherwise (and here virus transmission is of particular concern), the aberrant form of *P. minor* should be known as *Pentatrichopus minor* forma *dorsalis*.

Although it is advisable at present to consider the four forms of *Pentatrichopus* as distinct species, such may not necessarily be the case. In the Northeastern United States, where sexuales occur most commonly, a greater complex of forms exists, and all forms may be potentially capable of interbreeding. For example, Palmer (1952) noted copulations of a male similar to *P. fragaefolii* with a female of *P. minor*. In that area, none of the principal forms may possess a selective advantage. When parthenogenetic forms are transported to other areas, where sexual reproduction is not utilized, there would be no opportunity for genetic mixing and a more striking selection might occur.

Thus, only *P. minor* occurs in the southern part of Mississippi, and this species is absent from the Western United States. *P. fragaefolii* is not found in a large part of the Eastern United States. *P. thomasi* is more generally distributed. Large parthenogenetic clones developing in these areas are sufficiently different from the clones in other areas to invite specific designation. The striking morphological and biological differences exhibited by *P. jacobi* may actually indicate the true speciation.

REFERENCES CITED

Baerg, W. J. 1922. Eastern strawberry louse. Univ. Arkansas Agric. Expt. Sta. Bull. 179. 16 pp.

Balachowsky, A., and **L. Mesnil.** 1935. Les insectes nuisibles aux plantes cultivées, vol. 1. Paris: Ouvrage Honoré d'une Souscription du Ministère de l'Agriculture. 1,137 pp.

Darrow, G. M. 1937. Strawberry improvement. *In:* U.S.D.A. Yearbook of Agriculture for 1937, pp. 445–95.

Davidson, W. M. 1914. Plant louse notes from Cali-California. Jour. Econ. Ent. 7(1): 127–36.

1959. Personal communication dated at Orlando, Florida, 9 November (information concerning location of material from which sexual forms of *P. fragaefolii* were described).

Demaree, J. B., and **C. P. Marcus.** 1951. Virus diseases of strawberries in the United States, with special reference to distribution, indexing, and insect vectors in the east. Plant Dis. Reporter 35(12): 527–37.

Dicker, G. H. L. 1942. The biology of the strawberry aphid, *Pentatrichopus fragaefolii* (Cock.), with special reference to the winged form. Jour. Hort. Sci. 27(3): 151–78.

1956. Personal communication dated at East Malling, England, 17 November (general morphological information).

Forbes, A. R. 1959. Three new records of aphids (Homoptera: Aphididae) in British Columbia. Canadian Ent. 91(2): 121.

Forbes, S. A. 1884. Insects injurious to the strawberry. *In*: 13th Rept. State Entomologist of Illinois, pp. 60–180.

Frazier, N. W. 1960. Differential transmission of four strains of strawberry vein banding virus by four aphid vectors. Plant Dis. Reporter 44(6): 436–7.

Fulton, J. P. 1959. Personal communication dated at Fayetteville, Arkansas, 20 February (information concerning identification of Arkansas aphids).

Gillette, C. P., and **Miriam A. Palmer.** 1934. The Aphidae of Colorado. III. Ann. Ent. Soc. America 27(2): 133–255, figs. 209–333.

Greenslade, R. M. 1941. The migration of the strawberry aphid, *Capitophorus fragariae* Theob. Jour. Pomol. and Hort. Sci. 19(1–2): 87–106.

Hille Ris Lambers, D. 1953. Contributions to a monograph of the *Aphididae* of Europe. Temminckia 9: 1–177.

1958. Personal communication dated at Bennekom, Netherlands, 24 January (general morphological information).

Hodson, W. E. H. 1937. On the synonymy and biology of the strawberry aphid, *C. fragariae* Theob. (1912). Bull. Ent. Res. 28(3): 409–16.

Hottes, F. C., and **T. H. Frison.** 1931. The plant lice, or Aphidae, of Illinois. Bull. Illinois Nat. Hist. Surv. 19(3): 121–447.

MacGillivray, M. E. 1959. Personal communication dated at Fredericton, New Brunswick, 27 October (distribution of *Pentatrichopus* species).

Massee, A. M. 1935. On the transmission of the strawberry virus "Yellow Edge disease" by the strawberry aphid, together with notes on the tarsonemid mite. Jour. Pomol. and Hort. Sci. 13(1): 39–53.

Massee, A. M., R. M. Greenslade, and **A. J. Duarte.** 1938. Notes on the strawberry aphid (*Capitophorus fragariae* Theob.). Ann. Rept. East Malling Res. Sta. for 1937, 25: 209–12.

Miller, P. W., and **G. M. Darrow.** 1954. Two wild roses—alternative hosts for *Capitophorus fragaefolii* (Ckll.), the vector of strawberry viruses. Plant Dis. Reporter 38(2): 70–71.

Palmer, Miriam A. 1952. Aphids of the Rocky Mountain Region. The Thomas Say Foundation, Vol. 5. 452 pp.

Richards, W. R. 1959. Personal communication, Ontario, Canada, dated 20 October (distribution information on *Pentatrichopus minor*.)

Rorie, F. G. 1957. Resolution of certain viruses by the aphid vector *Capitophorus minor* Forbes. Plant Dis. Reporter 41(8): 683–9.

Russell, Louise M. 1958. Personal communication dated at Washington, D. C., 7 October (information on distribution of *Pentatrichopus* species).

Theobald, F. V. 1912. A new strawberry aphid. Entomologist 45(591): 223–4.

[3]Forest Insect Laboratory, Sault Ste. Marie, Ontario; Forest Biology Division, Science Service, Canada Department of Agriculture, Ottawa.

Thomas, I., and **F. H. Jacob.** 1940. The strawberry aphid, *Pentatrichopus* (*Capitophorus*) *fragariae* Theob., with notes on *P. potentillae* Walk. and *P. tetrahodus* Walk. Ann. Appl. Biol. 27(2): 234–47.
1941. British Aphididae. 1. The genus *Pentatrichopus* Börner (Hemiptera). Proc. Roy. Ent. Soc. London (B) 10(6): 107–23.
Whitehead, T., and **C. A. Wood.** 1946. Virus diseases of strawberries. I. The field problem in North Wales. Jour. Pomol. and Hort. Sci. 22(3–4): 119–33.

THE ANATOMY OF RHYTIDOPONERA METALLICA F. SMITH (HYMENOPTERA: FORMICIDAE)[1]

ROY M. WHELDEN
Haskins Laboratory, New Durham, New Hampshire

ABSTRACT

This descriptive study of this small species of *Rhytidoponera* treats of the integument; the flight muscles, as they change with age and disappear; the alimentary canal, with special attention to the pits in the ventral wall of the posterior part of the pharynx; all major glands, with comparisons between those of queens and workers; the reproductive systems of queens and workers; and the chordotonal organs and tissues of the proximal end of the metatarsus of the forelegs. The study was based on material from New South Wales which included 366 adult workers, some callow and some mature; 27 queens, some alate and others dealate; and 31 males. Sperm was found in the spermathecae of 21 of the workers. The worker caste includes two types of individuals, readily distinguishable on the basis of size. The thoraces of numerous workers contained late-stage pupae of an unidentified parasite, and in one instance a parasitic larva was encountered, possibly of the same species as these pupae.

The species of *Rhytidoponera* may be separated into two groups, one comprising the larger species, the other those of smaller size. *Rhytidoponera convexa* is one of the larger species; *Rh. metallica*, one of the smaller species. In addition to their obvious difference in size, these two species differ in another particular: in *Rh. convexa* there are no queens; normal queens occur exceptionally in *Rh. metallica*. Because of these differences, it seemed worth while to study in some detail the anatomy of each of these ants. That of *Rh. convexa* has been previously reported (Ann. Ent. Soc. America 50(1957): 271–282). This present paper describes comparable details of *Rh. metallica*.

This study of *Rh. metallica* is based on the examination of 366 adult workers (some callow, some mature), twenty-seven queens, and thirty-one males. The queens, all reared in the artificial nest, could be separated into three groups; (1) a few that were "alate," (2) some labelled "three months old" (these were all dealate), and (3) some known to be "at least one year old." In addition, about 70 workers were dissected in fluid, to remove for study whole organs or parts. All of this material was collected at Sutherland, New South Wales, Australia.

Examination of the worker material used in this study showed that it was possible to divide it into two groups, one of distinctly large workers, the other of much smaller workers. This difference in size was apparent in each of the parts and in each dimension, and was not due to the extension or telescoping of the segments of the gaster. Certain anatomical features appear to be correlated with the difference in size noted here.

[1]Accepted for publication March 26, 1960.

THE INTEGUMENT

Only one feature of the integument of *Rh. metallica* needs extended description: otherwise there is little difference to be noted between the two species. The one feature that differs is the stridulatory area. In *Rh. convexa*, this area was found to be circular or broadly oval in outline; a triangular stridulatory area was only rarely found. In *Rh. metallica*, this area is invariably triangular in queens, males and workers. (fig. 1E, fig. 4A). In the queens, the average size was 424 μ broad and 238 μ wide; the largest one measured 490 μ broad and 270 μ wide, the smallest 330 μ broad and 194 μ wide. In the workers, the average dimensions are 438 μ broad and 174 μ wide; the largest area found was 465 μ broad and 180 μ wide; the smallest 385 μ broad and 128 μ wide. It may be noted that in another worker the stridulatory area measured 335 μ broad and 142 μ wide; these two small areas typify the variation in shape which this stridulatory area may show, it being a rather low triangle in some workers, and in others quite high. Another variable feature is found in the two lateral mar-

gins, which vary from some which are nearly straight, to others which are broadly rounded. The three angles are always rounded. If one reduces these stridulatory areas to area measurements, it is obvious that the queen's are almost always slightly larger than the worker's. The males have a much smaller area, the average size being 350 μ broad and 168 μ wide.

Observed with a hand lens or with a microscope of low power, the margin of this area is sharply defined; with higher magnification, the actual edge of the area is not so easily determined, there being a narrow zone of uneven width in which the surface ridges are intermediate between the fine ridges of the area proper and the coarser ridges of the surrounding integument. (The extent of this area is outlined in fig. 4A.) The dimensions given above are measurments of the inner area, in which the quite uniform parallel ridges are found. There is only slight variation in the number of ridges: in the workers, the average number is 8.5 per 10 μ; in queens, 9 per 10μ; in males, 8.5 per 10μ. One other characteristic of the stridulatory area is the complete absence therein of spines of any size: spines are fairly numerous in the surrounding area; and are occasionally found in the narrow transitional area, where they are always very small.

THE MUSCLES

The muscles of this ant offer only one detail that should be considered, that is, the flight muscles of the queens. As in other ants, the structure of the flight muscles is quite unlike that of other muscles in the body. Fig. 1A shows the appearance of a stained section of one of the larger muscles joining the thorax to the coxa, in both transverse and longitudinal sections; fig. 1D shows a transverse section of one of a group of small muscles in the same region. These muscles are those of a queen. Fig. 1B shows a transverse and a longitudinal section of a part of the flight muscle of an alate queen. The difference between the two muscles is quite striking, not only in the size of the component fibres, but in the appearance of the various parts. In each of the young queens, whether alate or dealate, the flight muscles have the same appearance. In the several queens designated "3 months old" a very great change is apparent (fig. 1C). No trace of flight-muscle fibres remains, but in place of each of the many rather large masses of fibres, a row of large, irregular objects is found. In these objects, there is no visible trace of cytoplasmic contents, but only a sharply defined cell wall on the inner surface of which a slight trace of substance occasionally remains. Only the number and position of these objects suggest that they are derived from the several masses of flight muscle fibres. In the queens designated "1 yr. old", the upper part of the thorax is devoid of any apparent content; dissolution of the flight muscles is complete.

The presence of the large masses of the flight muscles necessarily causes many organs normally present in this region to be displaced, a few of them laterally, but most of them into the lower part of the thorax. With the disappearance of the flight muscles, there is no change in the position of the several organs; the oesophagus, the aorta, the labial gland, and the muscles all remain in the lower part of the thorax, the upper part appearing to be quite empty.

THE ALIMENTARY CANAL

The alimentary canal of *Rh. metallica* is quite similar to that of *Rh. convexa*. There are, however, several rather obvious differences. In *Rh. convexa* it was noted that the dorsal surface of the infrabuccal pocket, when contracted, was creased along two lines to form three ridges. In *Rh. metallica* a similar contraction was frequently noted; but here the creasing was irregular and unequal, no obvious ridges resulting.

In *Rh. metallica* the inner surface of the pocket has the same reticulated surface, bearing small spines in the region near the opening. But in this species, the reticulations are smaller and more irregular, and the spines less numerous and smaller.

The contents of the pocket varied greatly in amount in the many workers; not infrequently the pocket was completely empty. This empty condition was particularly noticeable in the queens. In the males, there was no individual having an empty pocket: in nearly all cases, the male tended to have more material in the pocket than did the workers. In no case was any individual, worker, queen, or male, found to contain anything approximating a pellet. Much of the material in the pocket was recognizable as insect remains: fragments of antennae were often noted; occasionally a bit of leg was seen; muscle fragments were not uncommon; and small irregular particles of integument were numerous. Much of the material found in the pocket could not be identified.

The buccal tube and pharynx are very similar to the same parts in *Rh. convexa*. However, there is a tendency for the walls to be slightly thicker and more deeply pigmented; the transverse ridges and the rows of spines on the inner surface are smaller and less extensive. There are also startlingly abrupt changes, from zones which are thick and deeply pigmented to those which are quite thin and nearly colorless. This is especially noticeable in the posterior portion of the pharynx.

One feature of the pharynx of *Rh. metallica* should be noted particularly. This is found in the ventral wall, posterior to the area on which the last of the several muscles are attached to

the pharynx, and extends to the junction of the pharynx to the oesophagus.

In this part of the thorax wall there are many small pits (fig. 2A, B). The total number appears to vary somewhat, from 24 to 30. In some individuals the pits seem to be without any order, being scattered irregularly along the ventral half of the wall (fig. A, B_4, B_5); in other individuals, they seem to be in four to six ill-defined, longitudinal rows.

The pits vary slightly in shape. The most frequently observed are cylindrical, and circular in transverse sections (fig. 2, B_1, B_2, B_3). Occasionally pits will be found which are conical in shape, the opening in the exterior surface of the wall being sometimes twice as much as the diameter of the inner end. These also are circular in transverse sections. Very infrequently, pits having an elliptical transverse section are found. In nearly all of the many examples studied the pits are perpendicular to the surface of the wall: only rarely are some observed to be at an angle of 80° to as much as 65° to the surface, the angle always being such that the opening is distinctly posterior to the inner end of the pit. The average diameter of these pits is 4 μ–5 μ in all three forms (worker, queen and male): rarely, the diameter may be as small as 3 μ; occasionally, some will measure as much as 5.5 μ in diameter.

The inner end of each pit is closed by a thin membrane. This membrane shows three variant forms. In some examples, it is quite smooth and either flat or bulging slightly into the lumen of the pharynx. In other examples (and these are more frequent), a small conical papilla in the center of the membrane projects into the lumen: this papilla is never more than 0.5 μ long. In the most frequently observed examples, a small circular boss occurs in the center of the membrane, rising 0.2 μ–0.4 μ above the inner surface. This boss may be hemispherical or nearly cylindrical and flat-topped. Its diameter measures 1 μ–1.2 μ.

All attempts to find any tissues directly connected with these pits failed in the present study. In similar pits in other species of ants very fine nerve ends were occasionally found to enter the pit and extend up towards or to the closing membrane. None could be found here. The only tissue noted is that shown in fig. $2B_2$, B_3, where rather coarse sparsely branching filaments were found in contact with the pharynx wall.

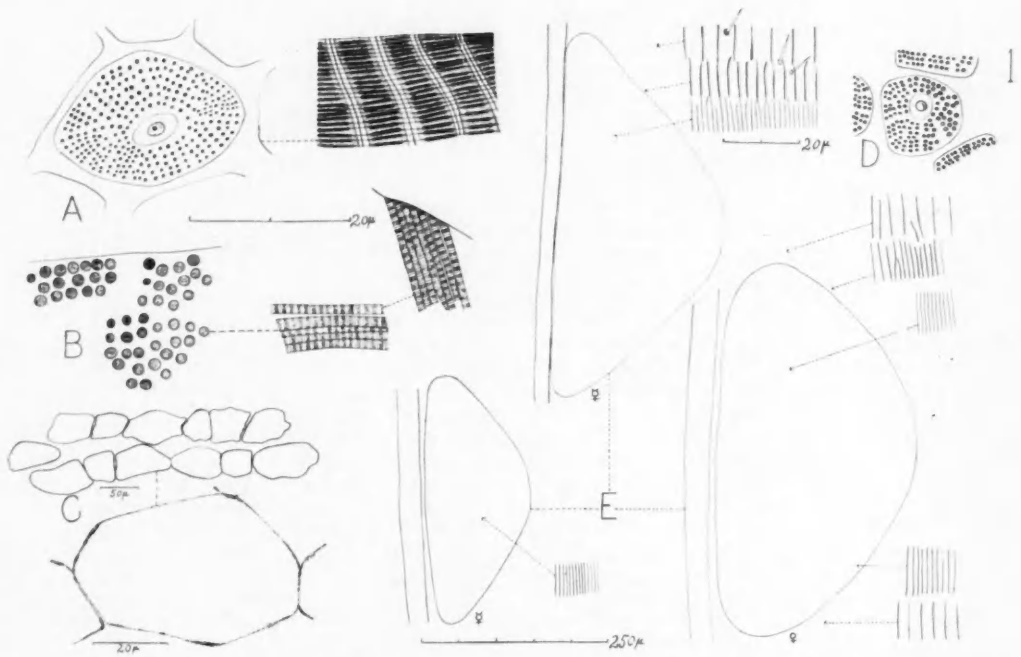


FIG. 1.—The flight muscles and the stridulatory area. A.—Transverse (at left) and longitudinal (at right) sections of a muscle of the base of the leg of a queen. B.—Transverse (at left) and longitudinal (at right) sections of a portion of the flight muscle of an alate queen. C.—Longitudinal section of a portion of the tissue replacing the flight muscle in a queen three months old; and a single unit of this tissue, more highly magnified. D.—Transverse section of a muscle of the base of a leg of a worker. E.—Outlines of three stridualtory areas, with details of the striae occurring in the areas indicated by the arrows.

Associated with these filaments were many nuclei, 3.5 μ–6 μ in diameter, with a cytoplasmic envelope so thin as to be all but nonexistant.

The oesophagus has the same structure as that of *Rh. convexa*, a thin-walled tube varying in diameter from one region to another and in different individuals. The inner surface of the wall of the oesophagus is quite unarmed. The muscle layer surrounding the oesophagus is very thin, with widely separated fibres.

The crop also has a structure almost identical with that found in *Rh. convexa*. However, in the *Rh. metallica* examined in this study, the number of individuals having a crop fully distended or nearly so is much smaller than those found to be so in *Rh. convexa*. This is especially noticeable in the queens, in which the crop was found almost invariably to be completely collapsed or nearly so.

The remaining parts of the alimentary canal—the proventriculus, stomach, intestine, and rectum—are so like those of *Rh. convexa* that little attention need be given them here. The number of rectal papillae may be either six or, less frequently, three; whether six or three, there seems to be little difference in the size of each papilla.

THE GLANDS

The Mandibular Gland (fig. 2C, C_1, C_2, C_3).—This gland is very similar to the gland in *Rh. convexa*; yet in nearly all details, there is a slight but obvious difference, often not easily described. The secretory part of the gland is a small hemispherical to ellipsoidal mass of 10 to 20 cells, and measures from 90 μ x 75 μ x 50 μ to 60 μ x 45 μ x 40 μ. This cell aggregate is usually smaller in the males and contains a smaller number of cells than is found in the gland in workers and queens. The component cells vary greatly in size, those near the center of the mass being rather larger than those near the edge. This mass of cells is located posterior to the base of the mandible and near but seldom in contact with the integument.

Almost completely enveloping this mass of cells, the chamber of this gland appears as an irregular pouch, very variable in both size and shape. The wall of this chamber is very thin, 0.2 μ–0.6 μ, showing its extremes in all but the areas immediately surrounding the many small nuclei, which measure 7.5 μ–9 μ x 3 μ–4 μ x 2 μ–2.5 μ. The variation in the size and shape of this chamber may vary according to the amount of secretion it contains. At times it is quite rotund and nearly smooth in outline; in other examples the wall is very much wrinkled, the entire chamber appearing collapsed.

From the "upper", usually narrower, end of each cell, a slender duct, less than 1 μ in diameter, passes over but never in contact with the surface of the cells. The several ducts converge to form a rather compact group which turns outward at its "lower" end to open in a small cribellum near the lower part of the group of secretory cells. The pores of this cribellum are irregularly grouped, and slightly more than 1 μ in diameter (fig. $2C_2$, cr).

When the chamber of this gland appears collapsed, it seems gradually to become an irregular tube which extends forward into the base of the mandible; when the chamber appears swollen and smooth-walled, the change into the narrow tubular portion is most abrupt and very obvious. The wall of this tubular portion is usually characterized by numerous irregular circumferential wrinkles. The actual opening occurs through the outer part of the mandible, near its base.

The Maxillary Gland.—The cells of this pair of glands form an irregular layer over the upper half of the infrabuccal pocket. They vary greatly in size, in shape, and in position. In some examples these cells are widely separated and rotund; in others the component cells are densely massed, becoming angular, and very irregular, occasionally with a long narrow outgrowth from the lower side. In all cases the cells always occur in a single layer, not as a compact mass. The cell dimensions vary greatly as shown by the following measurements: 50 μ x 46 μ, 44 μ x 24 μ, 42 μ x 17 μ, 33 μ x 28 μ, and 33 μ x 33 μ. There is little difference in the size of the glands and the number of component cells in queens, workers, and males.

The Corpora Allata.—These are somewhat variable in size, but always ellipsoidal. A rather narrow one measured 36 μ x 19 μ; a broad one 39 μ x 27 μ. Each contains about 18 spherical nuclei 6 μ–10 μ in diameter.

The Postpharyngeal Glands.—Each of this pair of glands, as in *Rh. convexa*, has many rather coarse irregularly dividing branches nearly all of which extend anteriorly or laterally from rather large irregular vesicles on either side of the anterior end of the oesophagus.

The Salivary (Labial) Gland (fig. 2D, D_1, D_2, D_3).—This large gland comprises the secretory part found in the anterior two-thirds of the thorax and the duct extending from this secretory portion to a small elliptical to circular opening near the middle of the labium.

This duct varies noticeably in structure from its anterior to its posterior end. The anterior end of the duct is a slender tube having a smooth inner surface and no apparent cellular layer externally. Posterior to this smooth region and extending back nearly to the posterior margin of the brain, the duct very gradually increases in diameter, as does the central lumen, and is now surrounded by a very obvious cellular sheath 2 μ–3 μ thick. In this cytoplasmic sheath, there are many small ellipsoidal nuclei, 2 μ–4 μ long and 1.5 μ–2 μ in diameter (fig. 2D). Near the midpart of the head, the diameter is 14 μ–15 μ, near the back of the head, it is 16 μ–18 μ. Passing into the anterior thorax, the duct increases

slightly, to 20 μ–23 μ in diameter. The lumen usually becomes somewhat smaller: in the posterior part of the head, it is 12 μ–13 μ in diameter, in the anterior thorax, 9 μ–10 μ. A very noticeable change occurs in the cytoplasmic layer surrounding the lumen: in the posterior part of the head, it appears to be very faintly vacuolate; in the anterior part of the thorax, this vacuolation becomes increasingly obvious. Here also the nuclei, still ellipsoidal, are much larger, measuring 7 μ–11 μ x 5 μ–6 μ: and the central lumen, instead of conforming to the curves of the duct, becomes a rather tortuous or sinuous tube (fig. 2D$_1$). This duct here divides into two branches, which may gradually diverge laterally and pass downward or may turn abruptly outwards to a point near the lateral wall of the anterior thorax and then gradually pass downward and posteriorly to the secretory part of the gland. In this part of the duct, the diameter becomes rather variable, from 40 μ–48 μ or rarely even larger, with the lumen measuring 16 μ–20 μ in the workers. In the queens, the dimensions of this part of the duct are considerably smaller than those of the workers, being 27 μ–30 μ in diameter, with the lumen 11 μ–14 μ in diameter. The annulations on the inner wall of the lumen are now noticeably thicker and 1.5 μ–2 μ apart. The cytoplasmic layer is now exceedingly vacuolate and the nuclei smaller and smaller until near the posterior end

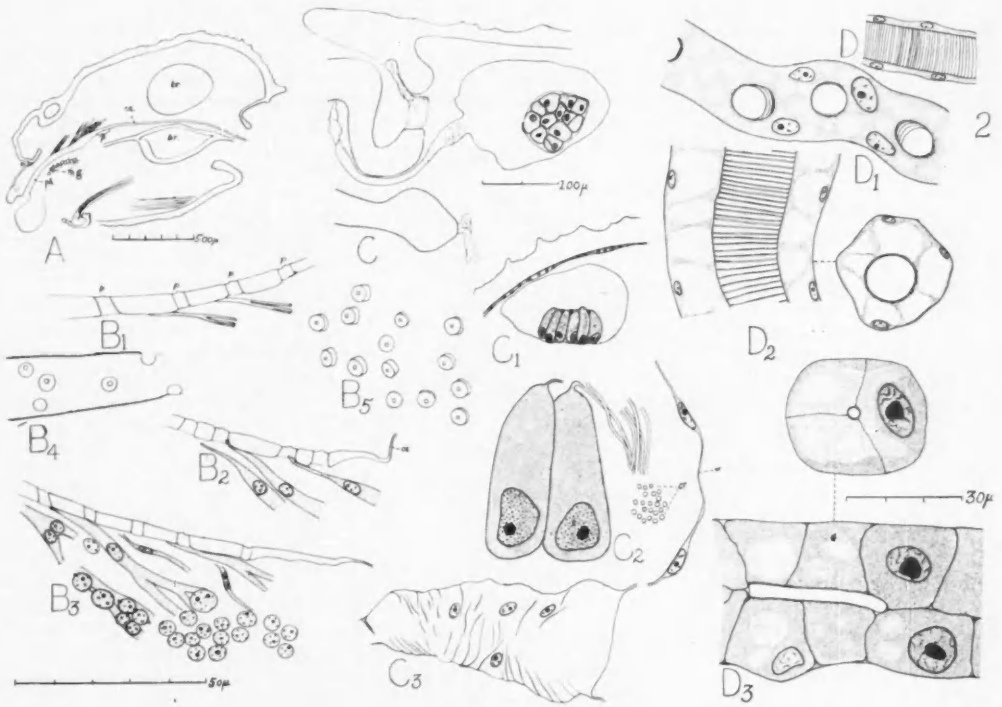


FIG. 2.—The posterior pharynx wall, the mandibular gland, and the labial (salivary) gland. A.—Diagrammatical section of head, showing pharynx (ph), oesophagus (oe), brain (br), and maxillary gland (m.g.) of a worker. B$_1$.—A portion of the wall of the posterior pharynx of a worker, showing four pits (p), and two of the slender strands occurring here. B$_2$.—Similar to B$_1$, but of the region where the pharynx joins the oesophagus (oe). B$_3$.—Another pharynx, this one showing five pits, and more extensive portion of the associated tissues. B$_4$.—A portion of a tangential section of the wall of the pharynx, with six pits, three of which show the central bosses on the membrane closing the pits. B$_5$.—A dissection of the ventral wall of the posterior portion of the pharynx, showing the number and distribution of the pits. C.—The mandibular gland, showing the small mass of secretory cells, the large chamber abruptly narrowing to an irregular tube passing into the base of the mandible. C$_1$.—A section of the mandibular gland approximately at right angles to that shown in fig. C. C$_2$.—Two of the secretory cells of the mandibular gland, with some of the ducts and the cribellum formed by the duct openings through the wall of the chamber; cr = cribellum. C$_3$.—Section of the wall of the base of the tube extending forward into the mandible and a portion of the thin wall of the chamber of this gland; w = wall of chamber of gland. D.—Duct of the labial gland, near the anterior end. D$_1$.—Longitudinal section of the labial gland duct in the anterior thorax. D$_2$.—Longitudinal and transverse sections of the duct of the labial gland, near its junction with the secretory portion. D$_3$.—Longitudinal and transverse sections of a secretory branch of the labial gland.

of the duct, they measure 3.5 μ–5 μ x 1.2 μ (fig. 2, D_2). Near the posterior end of the duct, the lumen rather abruptly decreases, the duct itself remaining large and the cytoplasm vacuolate.

The secretory part of the labial gland is quite variable, being formed sometimes of many rather long, irregular, widely separated lobes and sometimes a compact mass of irregularly convoluted branches. The latter is the usual appearance of this part of the gland in the queens, and is less frequently found in the workers. The lobes vary greatly in length, but are usually quite long. One lobe, teased out as straight as possible, was more than 1 inch long.

The several lobes of the secretory portion seldom branch except at the very base. There, branching occurs sparingly and irregularly; the branches extend anteriorly or vertically and to a limited extent posteriorly also, but are usually so twisting and entangled that it is difficult to determine the exact extent of each lobe. The lobes vary greatly in diameter, not only from one point to another in a single lobe, but also between the several lobes of a single individual. There is also a very obvious difference in the diameters of these lobes in workers, queens, and males.

In workers the diameter of the lobe is from 32 μ–43 μ, that of the central lumen 3 μ–4.2 μ; in the queens the diameter averages 28 μ, the lumen 5 μ; in males the diameter of the lobe is 27 μ–36 μ, of the lumen 3 μ. The compact massing of the lobes of the secretory part of the labial gland of the queen is perhaps caused by the pressure of the large mass of flight muscles which necessarily results in the other organs of the thorax being rather crowded in the lower part of the thorax. Because of this and the resulting compact mass of the labial gland, it becomes rather difficult to get true transverse sections of the lobes of this gland (fig. $2D_3$). The cytoplasm of the large irregular cells of these lobes is faintly vacuolate; the nuclei are ellipsoidal, and 7 μ–15 μ long and 5 μ–10 μ in diameter.

The Metasternal Gland (fig. 3).—This is another of the larger glands found in this ant. It extends forward in each side of the posterior part of the thorax, its anterior end just below or near the third thoracic spiracle. Of its three parts—secretory cells, ducts, and chamber—the secretory cells are the least variable, both in the workers and in the queens. It was not found in any of the males examined in this study. In the workers, the secretory cells—over 100 in each gland—form a mass 250 μ–350 μ in length and 100 μ–130 μ in diameter. This mass almost invariably comprises a single layer of contiguous cells in the form of an ellipsoidal or conoidal sac. In the queens, the cell mass is noticeably larger, being formed of approximately 200 cells. The cells vary both in size and in shape. Some are small and subspherical, and measure 25 μ–30 μ x 20 μ–28 μ; others are more elongate and measure 30 μ x 16 μ to 34 μ x 14 μ. Each cell contains a single usually nearly spherical nucleus 11 μ–14 μ in diameter; an occasional cell has an elongate or irregular nucleus measuring 6 μ–8 μ x 10 μ–11 μ.

From each cell a slender duct, 0.8 μ–1.2 μ in diameter, passes into the space within the cell layer. These ducts pass posteriorly through this region, gradually coming together to form a dense strand as they near the posterior end of the mass. At the posterior end, the many ducts separate slightly to open through the wall of the chamber of this gland. Together these openings may form a uniformly dense cribellum (fig. $3C_2$), or they may be separated to form a very loose, irregular aggregate. The total area of the cribellum may be nearly circular and 24 μ–26 μ in diameter, or it may be very irregular and measure 38 μ–40 μ x 30 μ–32 μ (fig. $3C_1$). The actual openings through the wall of the chamber are 1.7 μ–2 μ in diameter.

It is difficult to describe with any accuracy the shape of the chamber of the metasternal gland, partly because it is very irregular and partly because the variation is so great. Sections cut at various angles give a confusing variety of figures. Only by examination of serial sections does the shape become at all clear. Definitely, it may be called irregular. Against the wall of the thorax, it conforms to the outline of that wall, but since the outer surface of the wall has several rather coarse rugosities which may be reflected slightly by the inner surface of the wall, so the adjacent surface of the chamber may be irregular.

This chamber is always elongate and most frequently is more or less clearly marked by two unequal uneven constrictions, which may be made more obvious by rather coarse bends of the chamber. One result of this is that sections often show two or three unequal, apparently separate, cavities (fig. 3A, g.c.). The largest of these, the anterior one, may measure up to 200 μ in length and 70 μ–90 μ in diameter. Fig. $3E_{1-4}$ gives some idea of the variation in size and shape of this part of the gland, these being outlines, drawn to the same scale, of dissections of the posterior part of the thorax. The opening of this chamber occurs in the posterior end and is either circular, and 55 μ–70 μ in diameter, or ellipsoidal, and 70 μ x 60 μ in size.

The openings of the ducts through the wall of this chamber are always found in the dorsal or inner surface, just posterior to the constriction that marks the posterior end of the large anterior part of this chamber (fig. 3A).

In this study, the hypodermal layer of cells was often found to extend over at least a part of the wall of this chamber (fig. 3A, A_1, h).

Glands in Fourth and Fifth Gastric Segments (fig. 4C).—In contrast with *Rh. convexa*, where these glands are fairly large and several cells thick, in *Rh. metallica* they are quite small and usually only one or rarely two cells in thickness. Here, also, their structure is such that it is practic-

ally impossible to get a section that will show all desired details; the several parts seem never to be in a single plane.

The first pair of these glands (when there are two pairs), occurring in the fourth gastric segment, may comprise as few as 8 cells in each gland of the pair, but is usually 12 to 15 cells. Quite frequently, these cells occur as a single layer; or each gland may be two cells thick in the anterior and a single cell thick in the posterior part. Almost invariably, these cells form a concave mass conforming to the inner surface of the upper wall of the fourth gastric segment. Each cell gradually narrows (ventrally) into a rather short tortuous duct 1.4 μ–2 μ in diameter. The cells vary greatly in size and in shape, from small cells scarcely 30 μ in maximum dimension to some measuring up to 40 μ–75 μ in maximum dimension. Most frequent dimensions are 40 μ–50 μ. Almost invariably, the margin of the glandular mass from which the ducts arise has a very ragged or toothed appearance. The ducts are usually 50 μ–60 μ long. They open separately through the membrane connecting the fourth to the fifth segment.

A second pair of glands, similar to but much smaller than the pair just described, occurs in the fifth gastric segment. When present, it may very rarely comprise as many as eight cells; four to five cells are more frequently found; and in some individuals, there is but a single cell to each gland of the pair.

These glands are usually slightly larger in the queens, there being up to 18 to 20 cells in each of the pair. Neither the cells nor the ducts are larger than those in the workers. In the males, the glands are about equal in size to those in the workers, but always present a more ragged appearance, with the component cells tending to be distinctly separated.

In each of three succeeding segments of the gaster in the males, there is a pair of glands. These glands differ from those described above in having the component cells arranged in a single

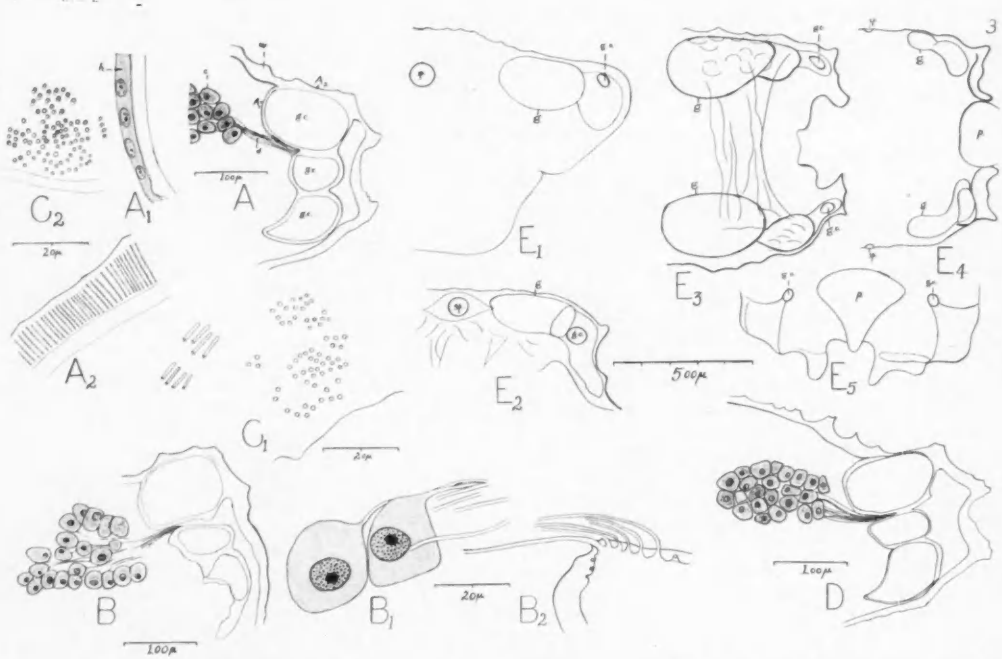


FIG. 3.—The metasternal gland. A.—Section of the posterior part of the thorax, showing the thorax wall (w), the metasternal gland chamber (g.c.), a few of the secretory cells (c), and the ducts (d) from these cells. A_1.—A detail of the wall of the gland chamber in the region indicated in fig. A, showing a hypodermal layer (h) over this region. A_2.—A detail of the thorax and chamber wall, in the region indicated by A_2 in fig. A. B.—A section from another worker, cut at a slightly different angle. No hypodermal layer occurred over the chamber in this worker. B_1.—Two of the secretory cells of this gland, and part of the ducts from the secretory cells. B_2.—The openings of some of these ducts. C_1.—A group of duct openings through the chamber wall of a queen, showing their somewhat irregular distribution. C_2.—A group of duct openings through the wall of the chamber of a worker. D.—A section of a third worker; to be compared with fig. A. E_{1-5}.—All five of these figures are dissections of the thorax wall and the chamber of the metasternal gland beneath the wall, showing the location of the spiracle (sp), the opening of the metasternal gland chamber (g.c.), and the outline of the chamber itself (g); p=pedicel.

row, or rarely in two rows, the cells occurring singly and not in contact. The ducts from these cells are very short: their openings through the membranes joining the greatly modified posterior segments occur in very irregular rows.

The Poison Glands (fig. 4B).—These two glands are very similar to those found in *Rh. convexa*. One, the acid gland, is much larger than the other. In nearly all the material examined here it is a simple tube; only rarely are individuals noted in which the anterior end bears two rather short, often very unequal, lobes. The other, the alkaline gland, is invariably much smaller than the acid gland, and of very different structure.

The openings of the two glands occur in the base of the sting, that of the alkaline gland being always above that of the acid gland. In each gland the wall surrounding the opening, and for a short distance anterior to the opening, is formed of somewhat irregular elongate cells, each with a single, small, spherical nucleus, which radiates outward from the small central lumen. These may be greatly modified muscle cells. There is no sign of any striation.

Emerging from the base of the sting, the two glands turn upward, at the same time gradually diverging, until each has reached a point higher than the uppermost part of the bursa copulatrix. At this point, the acid poison gland, which is the larger of the two, turns forward to pass above the bursa copulatrix. The alkaline poison gland may turn forward also, or it may end at a level near that of the upper part of the bursa copulatrix: should it turn forward, it is invariably much shorter than the corresponding part of the acid poison gland, and very slender. The acid poison gland frequently ends just above the last ganglion of the central nervous system. More often, however, two rather conspicuous branches extend from its anterior end. These branches may be of equal length and diameter, or they may be distinctly unequal, both in length and in diameter. Usually they extend forward throughout their length; only rarely does one turn toward the rear.

The dimensions of the poison glands are rather variable. The diameter of the alkaline gland varies from 8 μ–17 μ throughout its length; the diameter of the acid gland is larger and much more variable, 30 μ–42 μ being the usual range found in much of its length. But occasionally, an ant will be found with the anterior part of the gland greatly enlarged, to a maximum diameter of 130 μ–150 μ; more frequently, the maximum diameter is 50 μ–75 μ. The diameter of the anterior lobes, usually uniform throughout, varies from 30 μ–78 μ.

The walls of these two glands have a very different structure and appearance. Excepting the short portion anterior to the opening, the wall of the alkaline gland is quite thin and contains a very few small discoid nuclei having a diameter of 1.4 μ–2 μ and a thickness less than 1 μ (fig. $4B_5$). The most conspicuous feature of the wall of this alkaline gland is the presence of many obvious narrow folds or thickened ridges extending circumferentially, in some cases as complete annulations but frequently of much shorter length. Nuclei appear to be absent or of very rare occurrence in this gland, excepting the modified area near the opening and a short transitional zone.

In sharp contrast with the alkaline gland, the wall of the acid gland is thicker and distinctly cellular throughout. In the lower part of the gland, the wall varies from 4 μ–12 μ in thickness, with many small spherical nuclei 3 μ–4 μ in diameter rather unevenly spaced in it (fig. $4B_3$). Walls delimiting the cells of this part of the gland are not always easy to see and in many cases seem to be completely lacking. More anteriorly in the gland the walls become thick, the nuclei gradually of greater size, being 5 μ–8 μ in diameter, and the cell walls very distinct. Throughout this part of the gland the central lumen is very obvious, usually having a diameter at least as great as the thickness of the surrounding wall and often greatly exceeding that size, at least in the anterior part of the gland. The anterior lobes of this gland are quite unlike the rest of the gland in one particular—the lumen of the lobe is very small, sometimes almost lacking. In these lobes, the cells are clearly delimited, and each contains a spherical nucleus 5 μ–8 μ in diameter.

The Reproductive System (fig. $4B_1$, B_2, fig. 5).—It should be noted that there is no difference (except in the number of ovarioles in each ovary and in the length of these ovarioles) between the reproductive system of the queen and that of the worker. Therefore it will not be necessary to describe the two forms separately. The parts to be considered here include the ovaries, the oviducts, the uterus, the vagina, the spermatheca and its duct, and the spermathecal glands and their ducts. In addition, there is the bursa copulatrix and the less easily defined genital entrance.

The ovaries of *Rh. metallica*, in the queen and in the worker, are not particularly conspicuous. In the workers, the number of ovarioles in each ovary varies considerably: the smallest number found is two, the largest number seven. These are extremes and found only rarely. Most frequently, the number of ovarioles in each ovary is three to five. An occasional worker has unequal ovaries, one having one more ovariole than the other. In the queens, the number of ovarioles varies from five to seven, and there is always the same number in each of the two ovaries.

The length of the ovarioles is as variable as their number and rather more difficult to measure. The longest ovariole seen occurs in a worker. This is exceptional; in general, the ovarioles in the workers are relatively short, those in the queens long. The ovariole of a worker is usually less than one-half as long as that of a queen.

Individuals with mature eggs (i.e., cells having

clearly identified membranes surrounding the cell) are quite rare; those with large oöcytes, surrounded by the follicular epithelium, are rather frequently found. In very few of the many examined is an individual, queen or worker, found with ovarioles having a uniform development of oöcytes. Most frequently, especially in the workers, oöcytes are found in a single ovariole, or in two or three when there are four or five ovarioles. As a rule, the queens show greater uniformity.

The number of oöcytes in an ovariole also varies very greatly; most frequently, especially in workers, there is only one oöcyte, often very large. There is one queen in which each ovariole (five in each ovary) contains a row of five to seven oöcytes. In the remaining queens, the ovarioles are similar to those found in the workers.

The oviducts, both the paired and the common one, vary very much in length and in diameter. In one individual, the diameter is very uniformly 5 μ–6 μ throughout the length of the ovariole; in another, it is 10 μ–12 μ (infrequently 18 μ–32 μ) in diameter; and in another, it varies from 5 μ in one region to 10 μ–15 μ in another. The overall length is from 245 μ to over 600 μ. The wall of the oviduct is quite uniformly thin, measuring 1 μ–1.6 μ thick. Longitudinal muscle fibres form a loose layer outside the wall, both in the paired and in the common oviduct. This layer is about 1μ–2.2 μ thick.

The Uterus (fig. 5A, B, C, H, K).—The gross appearance of the uterus varies so greatly that an exact description is difficult. It is an irregular tube connecting the common oviduct with the vagina. At times, it seems to be tautly stretched, appearing as a rather narrow, quite straight, tube; again it appears as a contracted irregular mass of tissue of rather indefinite shape. So the dimensions (length 130 μ–210 μ, diameter 30 μ–90 μ) become rather meaningless, especially as the diameter may be uniformly narrow, or uniformly

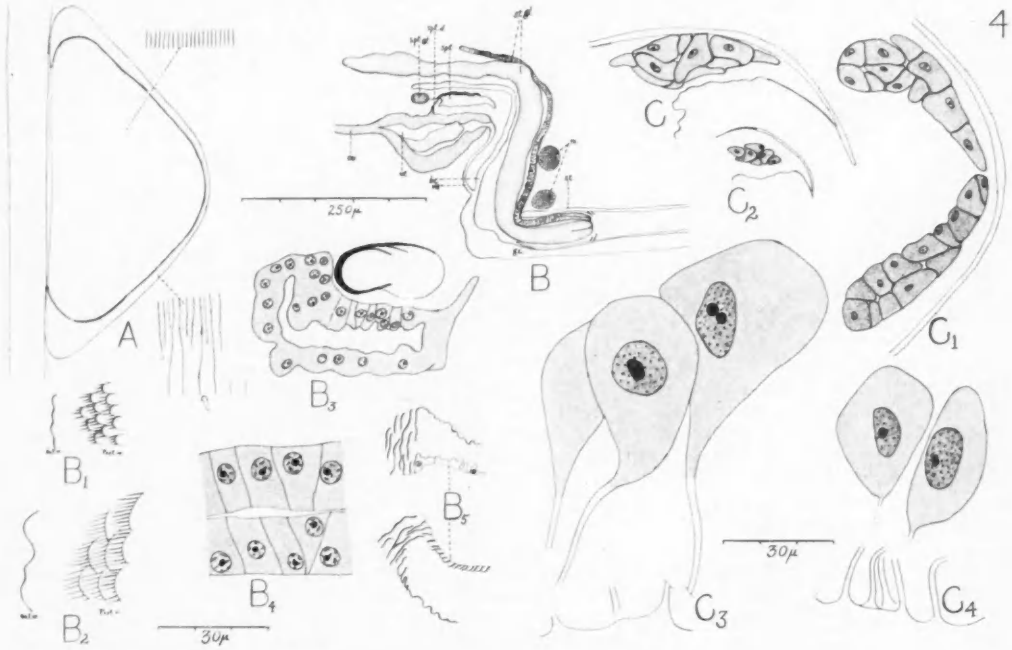


FIG. 4.—The stridulatory area, the sting glands, and the glands in the gaster. A.—The stridulatory area, with details of the striations occurring in this area. B.—Diagrammatic outline of the base of the sting (st), the sting glands (st.gl.), the genital entrance (g.e.), the bursa copulatrix (bc), the vagina (va), the uterus (ut), the common oviduct (ov), the spermatheca (spt), the spermathecal duct (spt.d.), the spermathecal gland (spt.gl.), and two transverse muscles (m). B_1.—Detail of smooth anterior (ant. w.) and spine-bearing posterior (post. w.) wall of the bursa copulatrix. B_2—Detail of the walls of the bursa copulatrix above the opening of the vagina. B_3.—Transverse sections of the two sting glands anterior to the base of the sting. B_4.—Longitudinal section of the larger (acid) sting gland. B_5.—Longitudinal sections of the smaller (alkaline) sting gland. C.—Longitudinal section of the gland occurring in the 4th gastric segment. C_1.—Transverse section of the same glands. C_2.—Longitudinal section of the smaller gland, occurring in the 5th gastric segment. C_3.—Detail of three cells of this gastric gland and their ducts, in a worker. C_4.—Detail of a corresponding gland in a male.

broad, or vary very much from one point to another. Sections show clearly that the wall may occasionally be contracted to form circumferential folds or creases, or it may form longitudinal folds in a most irregular manner.

The wall is always formed of three layers (fig. 5H): a very thin intima, and a layer of rather large uninucleate prismoidal cells, varying from 8 μ–32 μ thick (even in a single individual this layer may vary from 10 μ–18 μ in thickness), and an outer layer of rather loosely aggregated, circumferential muscle fibres. Over the upper part of the wall, this layer may be only 6 μ–10 μ thick, while below it may measure as much as 30 μ. It is quite variable in thickness from one point to another. The diameter of the lumen of the uterus varies very much. It may be scarcely 5 μ in a very narrow example; in another, the diameter may be 75 μ, or rarely even more. Commonly the diameter of the lumen of a single uterus may vary as much as this within a single specimen.

In one worker, an egg 110μ long and 60μ in diameter was found in the posterior part of the uterus.

It is through the anterior dorsal surface of the uterus that the spermathecal duct opens.

The Spermatheca (Fig. 5A, B, C, D, E, F, G).—This is an organ presenting an extremely variable appearance, yet its basic structure varies little except in size. No change in appearance can be correlated with queens and workers, or with the presence or absence of sperms, or with size. Most easily described are those which appear fully inflated, being rotund. It is then an oblate spheroid, varying much in size and little in shape (fig. 5C). In workers, spermathecae of this nature vary from small ones less than 50 μ long (which is the dimension from anterior to posterior margin) and less than 20 μ in depth. Large individuals may have spermathecae about 120 μ long and 105 μ–110 μ in depth. It is never possible in sectioned material to get a third dimension accurately. In those individuals measured herein, the breadth of the spermatheca is equal to or slightly less than the depth in fully inflated spermathecae. But, in by far the greatest number of individuals, the spermatheca appears to be partially or completely collapsed, or flattened dorsiventrally. In such individuals, the depth of the spermatheca may be as little as 20 μ.

The presence of sperms in the spermatheca does not determine its shape. It is true that a spermatheca containing sperms, whether in small or in large quantities, will invariably have an inflated or rotund shape. But so will many spermathecae in which there is no trace of sperms. Nor is size to be correlated with sperms. The largest spermathecae measured were some lacking sperms. However, no very small spermatheca was found to contain sperms. The dimensions of sperm-containing spermathecae are 80 μ–140 μ in length and 60 μ–110 μ in depth.

Twenty-one workers were found to be fertile; twenty of these were large workers, the remaining one was definitely a very small worker. The sperm mass, whether large or small, was always of very uniform density. Invariably, it was found to be near the opening into the spermathecal duct, into which a slender wisp of sperms extended. Small groups of 8 to 12 sperms were occasionally found in the lumen of the spermathecal duct and in the small pit that is found there. The total number of *Rh. metallica* fertile workers examined in this study is 5.43% of the entire number. This is to be compared with *Rh. convexa*, in which 7.57% are fertile.

The wall of the spermatheca could always be divided into two distinct but not sharply separated parts (fig. 5A, B, C, D, E). One of these, in the anterior dorsal region, is an area of noticeable thickness. This area is formed of prismoidal cells 16 μ–28 μ tall in the region of greatest thickness. The exact extent of this thick area is not easily measured, so gradual is the change from the thick to the thin part of the wall. Its extent may be nearly one-quarter of the total area of the spermatheca, but only rarely. Most numerous are spermathecae having less than an estimated one-sixth of the surface thickened. Many have thick areas much smaller than this, with an occasional spermatheca having the thick area not more than one-twentieth of the total area. These figures are at best only approximations. This is necessarily so, primarily because the change from thick to thin wall is usually so very gradual that no exact line of separation is possible. In the present study, the extent of the prismoidal cells is held to be the most reliable means of separation. The thin areas are composed of irregular polygonal cells less than 1 μ thick, except around the small nuclei found in this area. These nuclei are either ellipsoidal or discoidal and measure 1.2 μ–2 μ by 0.3 μ–1 μ. (fig. 5D, E show the appearance of this area.)

The spermathecal duct arises from the anterior part of this thickened area. Every feature of this duct is variable—its exact location, its length, its diameter, its lumen, and its wall. In most cases, the spermathecal duct arises near the anterior end of this thickened area and passes through it in a broadly curving arc that extends downward anterior to the spermatheca, and opens through the dorsal wall of the uterus near its anterior end. The total length of this duct varies from an extremely short one scarcely 40 μ long to those more frequently found, measuring 120 μ–150 μ in length. The wall varies very greatly in thickness, not only in different individuals, but also at different points in a single individual. Cross sections of the duct best show some of these differences. Usually these sections are circular, with a circular lumen within (fig. 5F$_2$,

detail at right). This lumen may be centrally located or it may be much to one side. Measurements in the first case may show a diameter of 16 μ–28 μ, with the central lumen 1.3 μ–4 μ in diameter. When the lumen, 2 μ–5 μ in diameter, is not in the center, the anterior part of the wall may be 13 μ–18 μ thick and the posterior part 6 μ–7 μ thick. In infrequent examples, the wall may be thin, the anterior part 6 μ thick and the posterior 3 μ or slightly less in thickness.

Two other features of the spermathecal duct should be considered. The first of these is the openings of the ducts of the spermathecal glands. These openings are found near the upper end of the spermathecal duct and will be described with the spermathecal gland. The other feature (occasionally lacking), in its most typical form, appears as a small cavity or pit in the inner surface of the posterior wall at some point in the upper half of the spermathecal duct. A gradual series of stages may be made between its complete absence and the more typical form most frequently observed. In its typical form as a small cavity or pit, it is directed diagonally downward into the posterior wall. Well-developed pits measure 4 μ–6 μ in diameter and are as much as 10 μ–12 μ deep.

The Spermathecal Glands and Their Ducts (figs. 5A, B, C, D, E).—The pair of spermathecal glands is found anterior to the spermatheca and

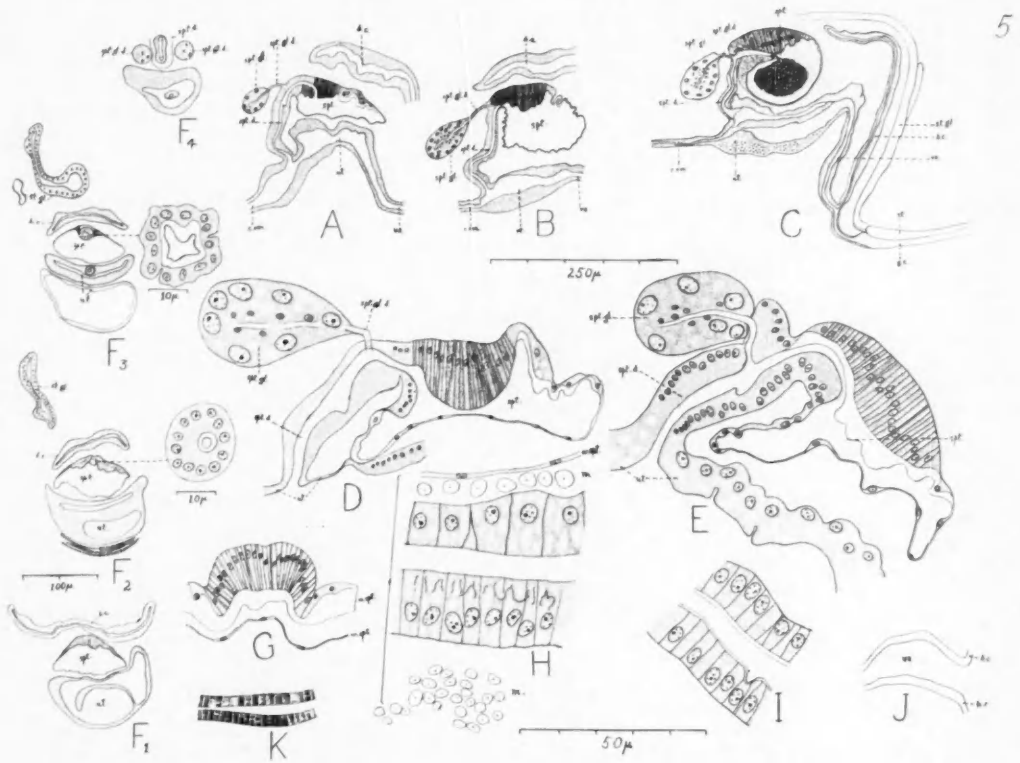


FIG. 5.—The reproductive system. A.—Median section of the reproductive system of a worker. B.—Median section of the reproductive system of a queen. C.—Median section of the reproductive system of a worker having sperms in the spermatheca. D. and E.—The spermatheca, the spermathecal ducts, the spermathecal glands and ducts of the spermathecal glands of two workers. F.—A series of transverse sections of the uterus, the spermatheca, and the bursa copulatrix. F_1 is in a plane near the middle of the spermatheca; F_2, near the anterior margin of the spermatheca; F_3, slightly anterior to F_2 and F_4 through the spermathecal glands. At the right of F_2 and F_3 there are enlarged details of the spermathecal duct. G.—Transverse section of the thickened area of the wall of the spermatheca and of the thin part of the wall below. H.—Longitudinal section of the wall of the uterus, showing muscles (m), wall cells and lumen, with a portion of the thin ventral part of the wall of the spermatheca (w.spt.). I.—Longitudinal section of the wall of the vagina in its midregion. J.—Longitudinal section of the wall of the vagina at its junction with the bursa copulatrix. K.—Two muscle fibres of the wall of the uterus. Spt., the spermatheca; spt.d., the spermathecal duct; spt.gl., the spermathecal gland; spt.gl.d., duct of the spermathecal gland; b.c., the bursa copulatrix; va, the vagina; ut, the uterus; c.ovi., the common oviduct; m, muscles; st.gl., the sting glands; g.e. the genital entrance; st, the base of the sting; w.spt., wall of the spermatheca.

its duct. They vary very much both in shape and in size. Most frequently, the shape of the glands is ovoid, gradually narrowing to the duct emerging from the posterior end. While the variation in size in workers is large, the two glands of each individual are very uniform in size, as the following measurements show: 32 μ x 16 μ and 32 μ x 17 μ; 32 μ x 21 μ and 31 μ x 31 μ; 50 μ x 28 μ and 50 μ x 26 μ; 36 μ x 24 μ and 35 μ x; 24 μ and 35 μ x 20 μ. In addition to the foregoing, glands measuring 54 μ x 37 μ and 62 μ x 31 μ were noted in two workers. In queens, these glands are somewhat larger than in workers, varying from 46 μ x 35 μ to 71 μ x 39 μ.

The structure of these glands is very similar to that found in *Rh. convexa*, there being several rather large nuclei, measuring about 6 μ–7 μ long and 4 μ–5 μ in diameter in the outer part, and many very small nuclei, measuring about 1.5 μ x 1 μ, around the small lumen of the gland.

Emerging from the posterior end of each gland is the slender duct, varying between 1.5 μ and 3 μ in diameter in nearly all cases, and with a length of 15 μ–50 μ. Usually the duct from each gland passes posteriorly, the pair gradually converging until they reach opposite sides of the thick-walled spermathecal duct. There the ducts turn inward and through the wall to open into the lumen on opposite sides and usually at a point near or slightly above the position of the pit described above. In less frequently observed cases the two spermathecal gland ducts pass posteriorly parallel one to the other and then turn abruptly inward to open through the wall. Very infrequently the two ducts gradually converge and pass into and through the wall rather close together on the dorsal or upper surface. In one apparently rare case the two ducts come together and join before reaching the wall of the spermathecal duct; in this case they pass through the wall as a single pore. In another apparently rare case, the pair of spermathecal glands are found in contact with the wall of the spermathecal duct. Here there is almost no spermathecal gland duct except through the wall of the spermathecal duct (fig. 5E).

The transition from uterus to vagina is quite abrupt and obvious. The very thin intima of the inner surface of the uterus becomes a much thicker layer in the vagina; there is no muscle layer surrounding the cellular layer. This cellular layer is much thinner and the cells comprising it are more slender, with smaller nuclei. Near the posterior end of the vagina, this cell layer gradually becomes thinner. The actual opening of the vagina is a small transversely elongated slit.

This opening is through the wall of a very characteristically shaped structure, the bursa copulatrix. This (fig. 5C, F) is a flattened pouch located between the reproductive system and the poison glands. The upper part of the bursa extends forward over the reproductive system. The length of this upper portion varies greatly: in some cases its most anterior point scarcely extends to the posterior margin of the spermatheca, in other cases it may extend beyond the most anterior part of the reproductive system; or it may end between these extremes. The breadth of this pouch varies also, not only from one region to another, but also from one individual to another. The maximum width is 100 μ–150 μ.

The wall of this pouch is moderately thick, and the inner surface sharply defined. The smooth surface of the anterior wall is frequently undulated in the lower part. There is an irregular layer of cells 2 μ–3 μ thick over the lower part of this wall. The inner surface of the posterior wall of the bursa is quite unlike that of the anterior wall. For a short distance the lower part is smooth. Above this smooth area the surface is completely bossed. The lowest of these bosses are small and nearly hemispherical, and each bears across its surface a row of five to seven small very acute spines (fig. $4B_1$). Gradually the bosses become broader and the spines longer and more numerous (fig. $4B_2$). Near the midpoint of the wall, this increase ceases and the bosses become smaller and smaller, with the row of spines also decreasing and finally ceasing completely. Small rounded unarmed bosses continue for a short distance after which the wall is quite smooth. The cellular layer over the outer surface of this wall is more uniform than that over the anterior wall, and 5 μ–6 μ thick.

At its lower end, the bursa is continuous with an illdefined space below the sting, which is the genital entrance.

LEG STRUCTURES

There remain to be described certain structures found in the legs. One of these, found only in the forelegs, is the antenna cleaner (strigil) and certain associated structures (fig. 6). The antenna cleaner is a small flat, pectinated spur at the lower end of the tibia. This spur has a flattened discoid base attached to the membrane joining the apical end of the tibia to the base of the metatarsal segment. A small irregular peg extends upward from the end of the wall of the metatarsus into the apical end of the tibia. The membrane noted above is attached around the edge of this peg. The flexion of the leg causes this peg to move in such a way that the attached membrane is pulled through a small angle and the pectinate spur attached to the membrane swings through an equal angle, thus bringing the spur against the wall of the metatarsus.

The surface of the metatarsus bears an abundance of rather stout spines, particularly near the upper end. There is, however, a narrow elongate area relatively free from spines in the upper part of the metatarsal wall. Spines that do occur here are slender and very acute. Along one

edge of this smooth area, there is a very regular row of stout close-set spines. It is against this area that the pectinate spur is pressed on flexion of the leg.

The wall of the metatarsus of an adult *Rh. metallica* averages 20 μ–25 μ in thickness. The canals through which the nerves pass to enter the bases of the surface spines are quite uniformly symmetrically shaped (fig. 6G, at right). The canals leading to the row of coarse spines are distinctly asymmetrical, the side nearest the smooth area of the metatarsal surface being straight, or curving slightly away from that area as the canal nears the outer surface of the wall. The base of the spine also curves slightly as it enters the nerve canal (fig. 6C, G, ca).

The inner surface of the metatarsal wall is more or less covered by a relatively thin hypodermis (fig. 6C, h), 1 μ–3 μ thick. Suitable sections show that this hypodermis is a reticulation of irregular cells (fig. 6D_2). Under the smooth area of the wall noted above, there is a conspicuously different layer composed of tall prismoidal closely aggregated cells (fig. 6B, C, G, p.c.; D_1). These cells are 25 μ–35 μ tall and 2 μ–2.5 μ in width. Through the wall over this mass of tall cells the numerous micropores are rather more conspicuous than those in the rest of the wall. These micropores almost invariably turn just above their base.

Two other tissues are found in this part of the leg: a single slender ligament (fig. 6C, l) arising from the end of the rather small muscle in the tibia and extending through the several tarsal segments; and the small nerve (fig. 6C, ne) from which very slender nerve fibres (n) extend out over the inner surface of the hypodermis to pass through the hypodermis and into the bases of the many surface spines. Similar slender nerves also pass over and through the aggregate of prismoidal cells.

Aggregates of prismoidal cells very similar to that described above are found in other segments of all six legs; these aggregates are much smaller

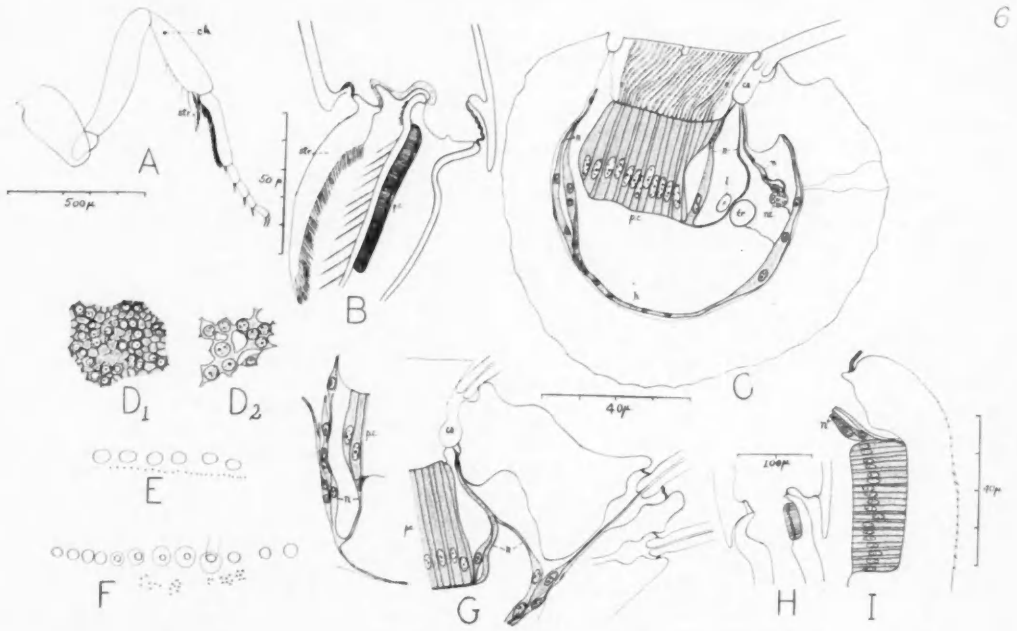


FIG. 6.—The strigil and associated structures. A.—Diagrammatic outline of the fore-leg, showing the location of the chordotonal organ (ch), and the strigil (str). B.—Outline of the strigil and associated structures. C.—Transverse section of the upper part of the first tarsal segment, showing wall (w), hypodermis (h), section of large nerve of leg (ne), nerves (n) to base of coarse spine, and the thickened area of prismoidal cells (p.c.). (l = ligament.) D_1—Transverse section of cells of the thickened area. D_2.—Transverse section of cells of the hypodermis, showing reticulate nature. E.—Pores and canals beneath rows of coarse spines. F.—A section slightly deeper in the wall than E. G.—A section near the midportion of the thickened area, showing (at the left) the margin of the layer and several nerve terminals, some to go to small surface spines and some to pass over the surface of the thickened area, and (at the right) the opposite margin of the thickened area and the several nerve endings occurring there, one passing into the lumen of a moderately large spine. H.—Outline of the upper end of the tarsus of a callow worker. I.—Detail of the thickened area of the hypodermis and of some nerve terminals of a tarsal joint of a worker; tr = trachea (in transverse section), p.c. = prismoidal cells, str. = strigil.

and the component cells somewhat shorter than those in the larger mass. Two of these smaller masses are shown in fig. 6H, I.

The Chordotonal Organ (fig. 7).—This organ is found in the upper part of the tibia of each of the six legs, about one-fifth to one-quarter of the distance from the upper end of the tibia. Its shape is always fusiform, though occasionally quite irregularly so. The most noticeable variation is in the ratio of the length to the width. In workers and in males, the length varies from three to five times the greatest diameter: in queens, the shape of this organ is more uniform, its length being about four times the maximum diameter. There is usually little difference between the chordotonal organs in the six legs of any one individual. The shortest organs are those which are at right angles to the long axis of the tibia; in general, the orientation is at an angle to the longitudinal axis, thus allowing for chordotonal organs having a length considerably greater than the diameter of the tibia. In infrequent cases, the chordotonal organ is somewhat curved, which also allows for a length greater than the diameter of the tibia.

The structure of this organ is quite constant, four very distinct regions being recognizable from base to apex. The most sharply distinct of these is the basal one, a rather small part separated from the others by a very obvious constriction. In some cases, the basal portion is very obviously formed of parallel filaments which may be distinctly spiraled, or not at all so. In all cases, this part of the organ contains many ellipsoid nuclei, some rather long and narrow (i.e., 6 μ x 2 μ), some small and slender (i.e., 3 μ x 1 μ), and some nearly rotund (i.e., 4 μ x 3 μ). The number of nuclei in this basal part is between 20 and 28.

The second recognizable part of this organ is that immediately beyond the constriction, and is characterized first by a gradual increase in diameter of that region and second by the presence of a number of very distinctive bodies, the scolops (fig. 7A, B, C, F_1, F_2).

The number of scolops present in a chordotonal body seems to be about 27 or 28. Because of their rather irregular arrangement, accurate counting is usually very difficult. In nearly all cases counted here, the number was as noted. In a few cases (all workers), there seemed to be about 21. The scolops are so grouped that it is difficult to cut a section that will include all of them. Figure 7B, cut at an acute angle, shows approximately their arrangement; fig. 7C, more nearly at right angles to the longitudinal axes of the scolops, shows more clearly how compactly some of them are aggregated.

Examination of the aggregate mass shows quite clearly that the scolops may be separated into two groups by an obvious difference in size. Fig. $7F_2$ shows some of each size, from a single chordotonal organ of a worker: the more numerous larger ones have a diameter of 2 μ–2.3 μ, the smaller ones a diameter of 1 μ–1.2 μ. The appearance of one of these scolops (in preparations stained with haematoxylin) is very constant. It seems to be a thick-walled cylinder at one end of which there is a small, subspherical globule of some substance staining very deeply with haematoxylin; from this globule a slender tail extends the entire length of the thick-walled part. In nearly all cases, this "tail" appears to be irregularly sinuous. The total length of the scolops varies somewhat: those with larger diameter may be 20 μ–30 μ long; the slender ones, 10 μ–15 μ long.

Above the scolops the chordotonal organ begins to narrow rather gradually. In this third part the most noticeable feature is the presence of many nuclei of two distinct types: comparatively large and ellipsoid nuclei, 7 μ–10 μ long and 4 μ–6 μ in diameter; and rather slender nuclei, 4 μ–8 μ long and 1.5 μ–2 μ in diameter. Sections suitably cut show clearly that the two groups of nuclei are sharply separated, the large ones in one group and the small slender ones in another (fig. 7D). The total number of these nuclei seems quite large; counting, however, seems to show that it may be about equal to those noted to occur in the basal part of the chordotonal organ.

Beyond the last of these nuclei the chordotonal organ continues as a slender, gradually narrowing tip which extends into an irregular pit in the inner part of the wall of the tibia. In this narrowing tip the only discernible feature is a number of ill-defined dark filaments extending nearly but not quite to the tip. The end of the organ may be straight and slender, almost sharply acute, or bluntly rounded, or it may be irregularly bent or contorted.

The pit on the wall of the tibia is also very variable. In some individuals it is almost exactly conical, in others nearly hemispherical, but most frequently it is quite irregular. At its greatest depth this pit may reach three-quarters through the wall. No evidence was found in this study that there is any actual opening through the wall of the pit.

Examination of a large number of chordotonal organs shows two other very obvious facts. One is that the organ seems to be "hollow". There is an irregular region in the central part of the organ which shows no sign of any structure, but does stain very faintly, suggesting the presence of some fluid substance.

The second fact is shown most clearly in transverse sections, but may be observed occasionally in longitudinal sections, at least in certain areas. This is the occurrence (in most of the specimens studied here, but not in all) of radiating plates connected by many slender strands—the whole giving a curious spongy appearance to the outer part of the organ. There is some evidence that

this occurs in individuals having a thicker, more deeply pigmented integument; that is, in older individuals. This "sponginess" seems to be limited to regions in which no nuclei are found.

One might wish to state that the chordotonal organ is formed of a compact group of filaments extending from one end to the other. It may be that this is so. The present study fails to show it. It does show that a slender branch issues from the single nerve which passes through

FIG. 7.—The chordotonal organ. A.—Transverse section of the tibia of the foreleg of a worker, showing the shape and structure of this organ. B.—Section of the chordotonal organ near its base, cut diagonally to show the number and distribution of the scolops. C.—Transverse section of the chordotonal organ from the middle leg of another worker. D.—Transverse section of the chordotonal organ at a point near its maximum diameter, to show the distribution of the large and small nuclei occurring in this region. E.—Longitudinal section from the same region as D. F_1.—Group of scolops from the chordotonal organ of a male. F_2.—Group of scolops from the chordotonal organ of a worker, showing the difference in size found in these elements. G.—Longitudinal section of the basal part of the chordotonal organ. H, I.—Apices of two chordotonal organs, and the pits in the tibia wall.

the femur. The slender branch passes into the tibia and down to the basal end of the chordotonal organ. Presumably, it joins the base of this organ. But it is possible that it may enter one of the hair canals that are rather numerous in this part of the leg.

PARASITES

Examination of the *Rh. metallica* collections available showed very clearly that many workers had distinctly larger thoraces than others. These megathoracic workers were found to have a parasitic organism in the thorax.

Forty workers with thoraces of normal size and forty of those having large thoraces were then measured. The normal thoraces measured 1,350 μ–1,500 μ long and 500 μ–550 μ high; the large thoraces measured 1,950 μ–2,050 μ long and 780 μ–820 μ high, and dissection showed a parasite to be present in each of the large thoraces. The parasites were 1,650 μ–1,900 μ long and 580 μ–620 μ high. Clearly the presence of a parasite is revealed by the size of the thorax, at least in the stage of parasite development reached in the ants examined in this study.

The parasite occured only in the thorax, where it was invariably found with its head in the anterior end. All parasites had reached the stage of advanced pupae, with one exception presently to be noted. All more or less completely filled the dorsal part of the thorax, displacing the organs normally found there. The oesophagus, aorta, nerve chord and trachea were crowded into the lower part of the thorax, the muscles pressed against the wall, and the lobes of the labial gland partly against the wall and partly into the ventral region.

The posterior end of the parasite might extend to the posterior end of the thorax, the metasternal gland then being displaced either laterally or ventrally.

With rare exceptions, slightly less developed, the wall of the parasite was closely pressed against the inner surface of the wall of the ant thorax, its shape therefore conforming to that of the ant thorax. Only the ventral part of the parasite showed clearly any segmentation, and even here the well-developed apodemes of the ant thorax modified the shape of the parasite. There was, however, some indication of a tripartite body, the rather large head being especially obvious. The thorax of the parasite showed three very distinct, large folds with very small ones separating them; the posterior part of the parasite was less clearly septate. The only obvious external feature was the presence, in three parasites, of two minute conical protuberances, 20 μ long and 15 μ in basal diameter, near the anterior end. In only one parasite was there any indication of mouth parts.

Some of the internal organs of the parasites were well-developed. Notable among these was the nervous system, with a rather large brain, three small but distinct thoracic ganglia, and a small elongate ganglionic mass posterior to them. The digestive system seemed to be very poorly developed; the muscular system was even less developed, only a few very small muscles being recognizable in the peripheral region. Fat body tissue was abundant and sharply defined. Other than these, the only organs present were two very large tubular glands.

Mention was made above of one parasite which differed from all the others. This one was a slender larva of 12 or 13 segments. It was about 500 μ long and 150 μ in maximum diameter. Possibly this was the larval stage of the same organism as the more numerous pupae.

ELEMENTE EINER SYSTEMATISCHEN AUFTEILUNG DER MACROMERINAE, by HERMANN HAUPT. Nova Acta Leopoldina, Bd. 21, No. 141, 74 pp., 33 figs., 1959. Price, DM 4.60.

This posthumous work on pompilid wasps was assembled from Haupt's notes and edited by Professor Rudolph Zaunick. In it are described 12 new genera and a number of new species of Macromerinae, that came into Haupt's hands subsequent to publication of his monograph (1927) of the European spider wasps. The bulk of the paper is concerned with the tribe Auplopidini; Haupt presents a key to the 27 genera that he assigns to this tribe; following this are keys to species, some of them translations into German of keys by Arnold to the African fauna and by Banks to the Philippine fauna, and some of them keys based on specimens available to Haupt; except for the translations the keys do not include all of the species, but only those known to Haupt.

This work will cause some taxonomic difficulties because Haupt based a number of his new genera on South American species; apparently he was not aware of Banks' publication on the South American spider wasps (1946), in which a number of new genera were described, and one or more of Haupt's genera will fall in synonymy. For example, *Ectemnagenia* Haupt (1959) is isogenotypic with *Priochilus* Banks (1944). Banks (1946) considered that *regius* F. belonged to *Priochilus*, but Haupt (1959) made it the type of his new genus *Acanthagenia*. *Parageniella* Haupt (1959) has as its type *rufofemoratus* Tasch., a species that Banks (1946) transferred to *Priophanes*; unless a misidentified genotype is involved, Haupt's name probably will not stand. The African genera *Dichragenia* and *Xysterocnemis*, which Haupt described (fully) as new in 1959, actually were validated by him in 1959 in an extremely abbreviated fashion. The one North American species that Haupt described in this work, *Deuteragenia fascipennis* from Illinois, is almost certain to be a synonym of *sayi sayi* Banks.

The taxonomic section is preceded by an obituary of Haupt by Professor Zaunick and a bibliography of his publications.

KARL V. KROMBEIN,
Entomology Research Division,
U. S. Department of Agriculture

A NEW-WORLD SUBGENUS OF BAMBOO-NESTING CARPENTER BEES BELONGING TO THE GENUS XYLOCOPA LATREILLE (HYMENOPTERA: APOIDEA)[1]

PAUL D. HURD, JR.[2,3] AND J. S. MOURE, C.M.F.[2]
Secção de Zoologia, Universidade do Paraná, Curitiba, Paraná, Brasil

ABSTRACT

A new subgenus, *Stenoxylocopa*, type species *Xylocopa artifex* Smith, is proposed for a New-World group of bamboo-nesting carpenter bees. Some aspects of the nesting habits of a new-described species, *Xylocopa nogueirai*, are reported, together with a summary of the literature pertaining to the nesting habits of the new subgenus.

In connection with a current systematic inquiry into the structural characteristics exhibited by the carpenter bees of the nearly cosmopolitan tribe Xylocopini, a group of quite closely related New-World *Xylocopa*, typified by *X. artifex* Smith, is so well differentiated from other similar units within the genus *Xylocopa* that it is treated as a subgenus in our forthcoming classification of the Xylocopini. On the basis of accumulated biological evidence, this group of species, like the unrelated Oriental subgenus *Biluna* Maa, selects for nesting purposes only the hollow cavities of internodally partitioned stems, especially those of bamboo. In southern China, according to Hoffmann (1938: 87) and Maa (1946: 68), these bamboo-nesting carpenter bees are popularly called "Chuk Fung" or "bamboo bees."

It is interesting that the presumed structural adaptations for nesting in these hollow culms are not equally shared by these two subgenera. Each appears to have developed a fundamentally different type or set of structures to facilitate nesting in the hollow-culm habitat. Similarly, some other unrelated groups of *Xylocopa*, which also nest in hollow stem cavities, do not possess coincident structural modifications of the type believed to be adaptively useful.

The primary objective of this paper is to place on record some biological observations made on an undescribed species of the new subgenus. In addition, the name of the new species is needed for a study of its larval morphology to be published shortly by Lic. Bernadete Delourdes Lucas of this university. Other studies are also underway on certain morphological features of the pupa and the adult by Dr. Warwick E. Kerr and his students in the Departamento de Biologia Geral, Faculdade de Filosofia, Ciências e Letras de Rio Claro, Rio Claro, São Paulo, Brasil.

The new species was discovered nesting in bamboo during a very enjoyable visit (February 8–13, 1960) with Dr. Paulo Nogueira-Neto and his family at their sugar plantation, The Fazenda Usina Estér, near Cosmópolis, São Paulo, Brasil. An account of these observations together with some other information relating to the nesting habits of this new subgenus follows the taxonomic discussions.

We are very deeply indebted to Dr. Nogueira, not only for placing at our disposal all the facilities of the fazenda, but also for his most helpful assistance in locating, collecting, examining, and photographing the nests of the new species, as well as those of other bees.

For certain identifications used in this paper, we are grateful to Dr. B. D. Burks, U. S. National Museum, Washington, D. C. (Leucospidae), Dr. Ralph J. G. Hertel, Cadeira de Botânica, Universidade do Paraná, Curitiba, Brasil (*Bambusa* sp.), and Lic. Ayrton de Mattos, Diretor, Secção de Botânica, Instituto de História Natural, Curitiba, Paraná, Brasil (*Chusquea bambusoidea* H. K.).

The type specimen of *Xylocopa surinamensis* Enderlein was very helpfully made available for study by Dr. B. Pisarski, Institut Zoologique, Academie Polonaise des Sciences, Warszawa.

Celeste Green, Senior Scientific Illustrator, Department of Entomology and Parasitology, University of California, Berkeley, kindly prepared the drawings, and the genitalic drawings were subsequently inked by Akira Dairiki of Curitiba, Brasil.

The description of the new subgenus which follows is presented in terms of the world *Xylocopa* fauna rather than the more restricted view (and hence use) that would result if it was based solely on the New-World fauna of *Xylocopa*.

Stenoxylocopa Hurd and Moure, new subgenus
(Figures 1–8)

Type species: *Xylocopa artifex* Smith, 1874, present designation.

MALE.—Body of small size (12–19 mm.),

[1]Accepted for publication March 28, 1960.

[2]The authors wish to acknowledge aid from the Campanha Nacional de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Rio de Janeiro, the Conselho Nacional de Pesquisas (CNPq), Rio de Janeiro, and the Instituto de Pesquisas da Universidade do Paraná, Curitiba, Brasil.

[3]Permanent address: University of California, Berkeley, U.S.A. Currently: Research Scholar, "Fulbright Commission," and Fellow, John Simon Guggenheim Memorial Foundation, New York, U.S.A.

rather slender and elongate, somewhat thickly pubescent on thorax, sparsely to moderately so elsewhere; vestiture chiefly grayish-black, but with some paler pubescence on legs and body undersurfaces; integument black, very feebly metallic in bright light; tegulae normally black, sometimes reddish; pale markings occur normally on mandibles near base, labrum, clypeus at sides, supraclypeal area (occasionally), and parocular areas nearly to posterior margin of vertex; wings nearly hyaline to lightly infuscated, weakly violaceous, sometimes faintly tinged with bronze, gold, green, and rose in varying proportions. Length of forewing including tegula 12–18 mm.

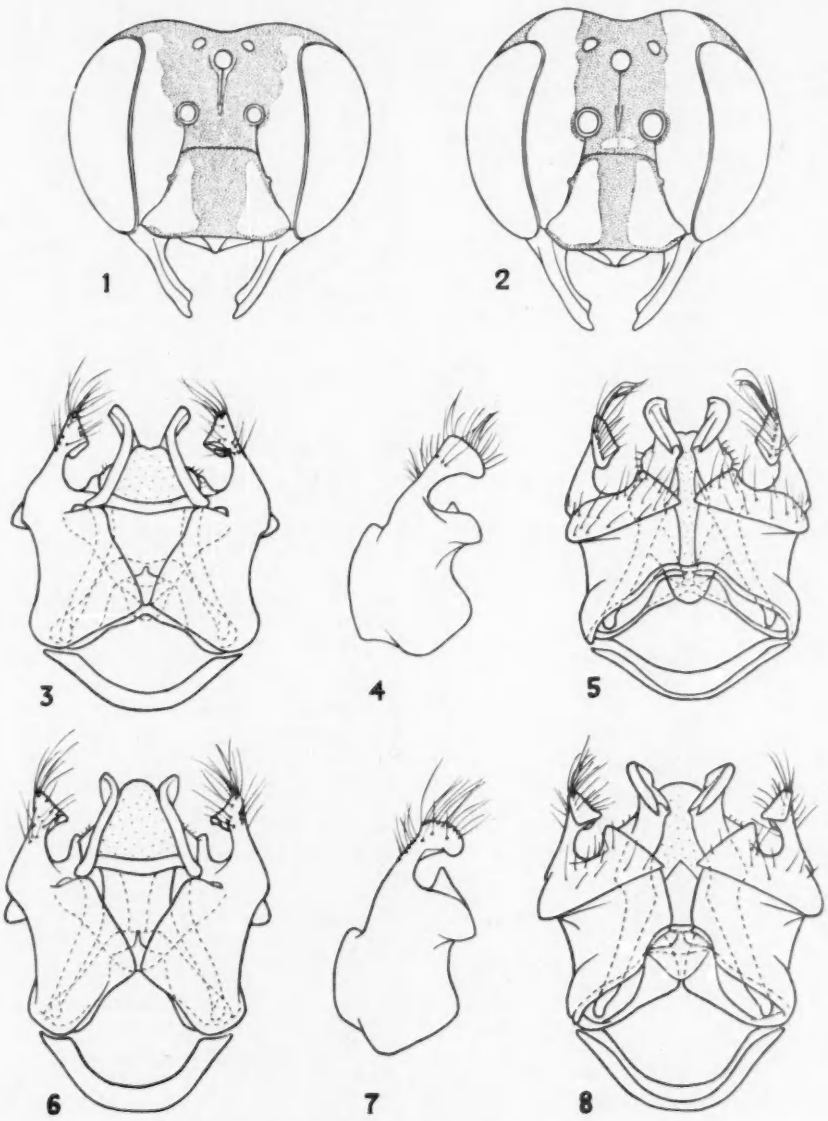
Head.—Eyes small, maximum width of eye, as measured from in front, considerably less than minimum upper interorbital distance, more convergent above than below or conversely; inner orbits clearly incurved, well removed from antennal sockets, separated from them by much more than length of a subantennal suture. Face broad, minimum interorbital distance greater than length of scape, broadest near middle, narrowed above and below. Vertex, as seen from in front, strongly elevated above upper eye margins, conspicuously depressed medially, posterior margin, as viewed dorsally, angularly produced forward; orbitoccipital distance long, longer than first flagellar segment. Malar area very short, minimum length reduced to a linear ribbon. Ocelli normal, situated high on face, posterior margins of hind ocelli removed from posterior margin of vertex by much less than distance across hind ocelli; anterior ocellus and antennal sockets of about equal diameter, without lateral swellings or ridges; interocellar distance a little greater than ocellorbital distance. Clypeus essentially flat, without a longitudinal median keel, sparsely punctate, scarcely more than three-fourths as long as broad, much longer than clypeocellar distance, dorsolateral sides weakly raised above level of adjacent parocular areas. Epistomal suture with transverse section obscured by fusion of clypeus and supraclypeal area, lateral sections concavely incurved. Subantennal sutures short, each much shorter than interalveolar distance. Supraclypeal area somewhat elevated, lateral sides rounded, raised above level of adjacent parocular areas. Frontal carina present, weakly elevated, cariniform, with a longitudinal sulcus basally, its apex much closer to upper margin of clypeus than to anterior tangent of median ocellus. Antennal sockets located much nearer to upper margin of clypeus than to anterior tangent of median ocellus; interalveolar distance longer than interocellar distance. Parocular areas without depressions, sulci, or carinae; clypeorbital distance less than minimum thickness of first flagellar segment. Apex of scape much surpassing level of upper eye margins; first flagellar segment approximately equal to or much longer than combined length of succeeding two segments, but significantly shorter than combined length of succeeding three segments. Mandible bidentate at apex, without a subapical inner tooth near middle of upper margin, lower margin, as seen from side, almost straight, outer apical tooth projecting much beyond lower mandibular margin; rear angle of mandible very near posterior eye margin. Labrum transverse, more than twice as wide as long, its apical margin weakly emarginate, longitudinal median carina present, strongly cariniform or trianguliform. Maxillary palpus six-segmented.

Thorax.—Posterolateral lobes of pronotum normal, not greatly expanded onto mesepisterna. Disc of mesonotum broadly impunctate medially. Parapsidal lines deeply impressed, nearly paralleling median line, approximately as long as first flagellar segment. Tegulae not prolonged posteriorly, their posterolateral thirds impunctate, glabrous, and shining. Scutellum, metanotum, and dorsal margin of propodeum exposed, as seen in profile, along same subhorizontally inclined plane; scutellum nearly flat. Metanotum moderately convex in profile, subangulately lengthened medially, maximum median length much longer than combined length of second and third flagellar segments. Forewing with three complete submarginal cells; third intercubitus strongly and angulately bowed outward. Basitibial plate present, its apex simple, situated before middle of tibia. Malus of antennal cleaner normal, sharply pointed, much longer than velum. Anterior coxal spines short, much less than length of scape. Middle and hind trochanters without spines or tubercles, however, inner ventral apex of hind coxa often acuminately produced. Ventral surfaces of hind femora somewhat flattened and broadened, without spiniform carinae or tubercles near base. Hind tibiae a little shorter than corresponding femora; each outer distal apex of middle and hind tibia armed with a tooth. Tarsi and claws normal.

Abdomen.—Propodeum steeply inclined, narrowly exposed subhorizontally along dorsal margin; triangular area absent, longitudinal median groove deeply excised, complete; propodeal spiracles large, unmodified. Dorsal surface of first metasomal tergum sloping forward, rounding into anterior surface; vertical fold of anterior surface linear, shallowly impressed, and not foveate above. Apical margin of first metasomal sternum rounded in outline, shallowly emarginate medially. Gradulus of first metasomal tergum obliquely curved away from anterior ventral margin of metasoma and continued posteriorly adjacent to lateral margins. Metasomal terga II–VI with graduli, each narrowly interrupted medially, straight and abbreviated laterally on terga II and VI, bent posteriorly behind spiracles on terga III–V; lateral pregradular area near spiracles densely hirsute. Metasomal sterna II and III with graduli, that on sternum II angularly deflected posteriorly at narrow medial interrup-

tion, that on sternum III scarcely visible, vestigial. Metasomal spiracles normal. Sixth metasomal sternum with a longitudinal median carina. Apex of gonocoxite simple, penis valves not pubescent apically (figs. 3–8).

FEMALE.—Body of small to nearly medium size (14–22 mm.), rather slender and somewhat elongate, moderately to thickly pubescent throughout, thickest on thorax and at sides and apex of metasoma, forming there a rather compact lateral fringe; vestiture brownish-black or black; integument black, paler below, with very feeble metallic reflections in bright light; tegulae black, sometimes reddish; wings lightly to strongly infuscated,



FIGS. 1, 3–5.—*Xylocopa nogueirai*, n. sp., male. FIG. 1, Anterior view of head. FIGS. 3–5, Genitalia; Fig. 3, dorsal view; Fig. 4, lateral view; Fig. 5, ventral view.
FIGS. 2, 6–8.—*Xylocopa artifex* Smith, male. Fig. 2, Anterior view of head. Figs. 6–8, Genitalia; Fig. 6, dorsal view; Fig. 7, lateral view; Fig. 8, ventral view.

violaceous or with brilliant hues of bronze, gold, green, and rose in varying proportions. Length of forewing including tegula 13–19 mm.

Head.—Eyes either more convergent above than below or conversely; maximum interorbital distance occurs slightly above level of antennal sockets; inner orbits weakly incurved, separated from antennal sockets by a distance equal to or less than interalveolar distance. Face broad as in male. Vertex, as seen from in front, very nearly straight across or slightly depressed medially, arcuate at sides, posterior margin, as viewed from above subangulately to angulately procurved. Malar area short, minimum length much less than that of second flagellar segment. Ocelli normal, without adjacent prominences, hind margins of posterior ocelli situated below level of upper eye margins; anterior ocellus approximately as large as lateral ocelli, slightly smaller than antennal sockets, its hind margin tangent to or slightly below a line drawn across anterior margins of lateral ocelli; interocellar distance shorter than ocellorbital distance, latter distance conspicuously shorter than distance between an antennal socket and nearest lateral ocellus; supraocellar pits deeply punctiform, somewhat craterlike, without a tooth within. Clypeus flat, evanescently keeled mediolongitudinally, approximately one-half as long as broad, shorter or longer than clypeocellar distance, dorsal lateral sides strongly and abruptly raised above adjacent parocular areas. Subantennal sutures, supraclypeal area, frontal carina, and antennal sockets as in male. Parocular areas weakly and subangulately raised along lower inner orbits, without parocular carinae; clypeorbital distance short, as in male. Apex of scape considerably surpassing level of upper eye margins. Mandible bidentate at apex, with an evanescent or vestigial subapical inner tooth near middle of upper margin; *outer apical tooth, as seen from side, considerably (nearly twice) narrower than the obliquely truncated inner apical tooth*, as determined by measurement across mandible at basal level of notch between them; rear angle of mandible situated in front of posterior margin of eye. Maxillary palpus six-segmented, as in male.

Thorax.—Disc of mesonotum broadly impunctate. Parapsidal lines long, more than one-half as long as first flagellar segment, converging toward median line. Scutellum unmodified, gently to moderately convex in profile. Metanotum obliquely to subvertically inclined, subangulately lengthened medially. Forewing, as in male, with three complete submarginal cells; third intercubitus weakly and subangulately bowed outward, its anterior portion more basad than posterior portion. Apex of basitibial plate asymmetrically bifid, situated beyond middle of tibia. Hind trochanter, as seen from below, arcuate along inner margin, not triangular in outline. Hind tibiae much shorter than corresponding femora; outer distal apex of middle tibia armed with a single tooth, that of hind tibia with two teeth, anterior one less strongly developed.

Abdomen.—Propodeum declivous, weakly arcuate in profile; triangular area present, large, well differentiated; longitudinal median groove complete, shallowly excised; propodeal spiracles large, unmodified. Dorsal surface of first metasomal tergum and vertical fold as in male; discal hairs of first metasomal tergum simple or at most sparsely plumose. Apical margin of first metasomal sternum rounded, weakly incurved medially. Gradulus of first metasomal tergum as in male. Metasomal terga II–VI without graduli; lateral pregradular areas adjacent to mesal border of spiracles on metasomal terga III and IV not densely and minutely punctured. Metasomal sterna II–IV with graduli, each moderately interrupted medially; dorsal and ventral carina of metasoma present, moderately to strongly evident; apical margins of metasomal sterna weakly to conspicuously pointed at middle; median longitudinal carina of sixth metasomal sternum elevated throughout much of its extent. Pygidial plate quite strongly diverging anteriorly, with a pair of subcylindrical, subapical lateral spines, without prepygidial denticles.

This subgenus, which ranges from Argentina (Province of Buenos Aires) to the United States (Arizona), contains four described species. Two of these, *Xylocopa artifex* Smith (1874: 289) and the new species, are based on specimens from Brazil. The other two species, *X. lehmanni* Friese (1903: 203) and *X. strandi* Dusmet y Alonso (1924: 54) were described from Colombia and Costa Rica respectively. At least three additional species remain to be described. Whether *X. colona* Lepeletier, 1841: 185 ("de Cayenne . . . la variété du Perou") is a *Stenoxylocopa* or a small *Neoxylocopa* is still uncertain, since the original specimens could not be located by one of us (Moure) in the three museums (Muséum National d'Histoire Naturelle, Paris; the Westwood Collection, Hope Museum, Oxford; and the Instituto di Zoologia dell' Universitá di Torino) which now maintain the major portions of the Lepeletier collection.

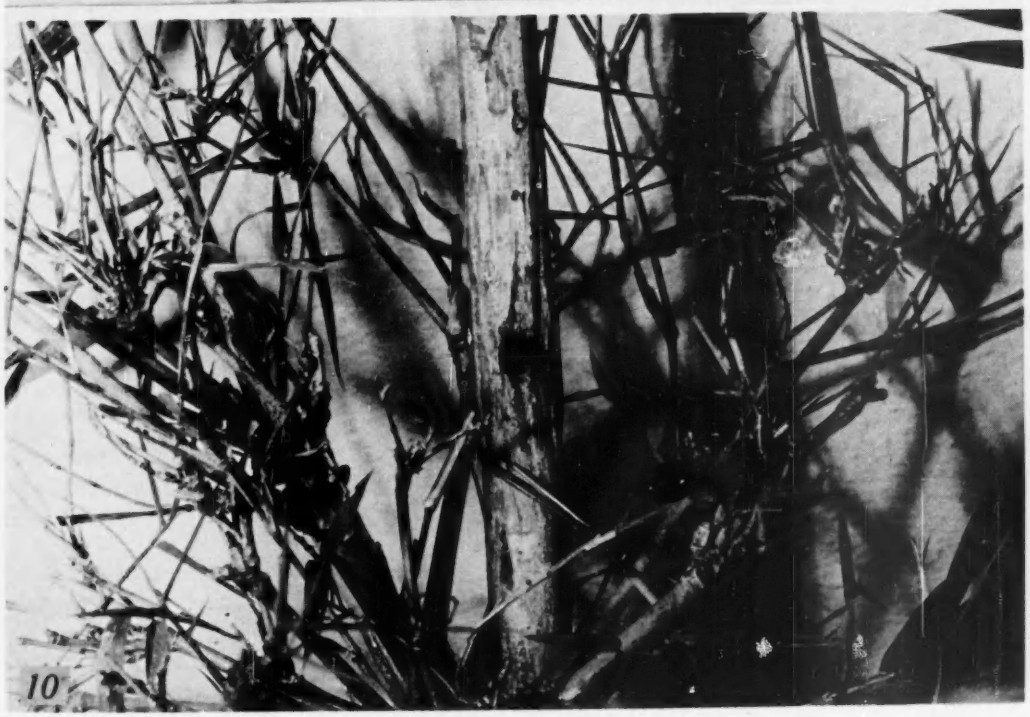
Although *X. surinamensis* Enderlein (1913: 163) was compared with *X. artifex* Smith at the time of the original description, a recent study of the type specimen reveals that it is a member of the subgenus *Neoxylocopa*. A full treatment of

EXPLANATION OF FIGURES 9 AND 10

FIG. 9.—Roadside clumps of bamboo in which the majority of *Xylocopa nogueirai* nests were located.

FIG. 10.—Bamboo culm showing the characteristic nest entranceway of *Xylocopa nogueriai*.

9



10

this species is to be presented in our revisional study of the American *Xylocopa*.

The subgenus *Stenoxylocopa* is most closely related to the American subgenus *Neoxylocopa* Michener. Like that subgenus, the sexes are quite dissimilar in appearance and often difficult to associate properly. Among the more important features shared by the males of these subgenera are the similarly constituted genitalia, especially the structure of the gonocoxites, the broad face, the strongly elevated and medially depressed vertex, the similar exposure of the scutellum, metanotum, and dorsal margin of the propodeum along the same subhorizontally inclined plane, and the high insertion of the antennae on the face, well above the middle of the eyes, so that the apex of the scape much surpasses the level of the upper eye margins. The females of *Stenoxylocopa* and *Neoxylocopa* share significantly the well-developed, longitudinal median carina on both the dorsum and venter of the metasoma, the abruptly elevated and highly polished upper lateral margins of the clypeus, the two teeth on the outer distal apex of each hind tibia, and the quite thickly fringed lateral sides of the metasoma.

In contrast with *Neoxylocopa*, the body of *Stenoxylocopa* is narrower and more elongate. In *Stenoxylocopa* the integument of the males is, excluding facial maculations, chiefly black, paling to piceous on some ventral parts, while that in the males of *Neoxylocopa* is largely ferruginous or fulvous as is also the vestiture. Structurally, the males of *Stenoxylocopa* differ from those of *Neoxylocopa* in the broadly impunctate, glabrous, and shining posterolateral thirds of the tegulae, the narrowly swollen dorsal margin of the clypeus which obscures the transverse section of the epistomal suture, the apically incurved margin of the first metasomal sternum, the essentially black scape, the nearly vertically inclined posterior face of the propodeum, and the much shorter first flagellar segment. The females of *Stenoxylocopa* are readily distinguished from those of *Neoxylocopa*, as well as from any other known *Xylocopa*, by the uniquely modified mandibles described above in italics. In addition, the upper margin of the mandible lacks the deep median notch so typical of the females in *Neoxylocopa*.

The subgenus *Stenoxylocopa* is not closely related to any of the Old World *Xylocopa*. It is of interest that Cockerell (1904: 30) was impressed by the "extremely strong superficial resemblance" between the males of this newly described *Xylocopa collaris binghami* from the Khasia Hills of India and those of the Neotropical *X. erratica* Smith (= *X. artifex* Smith).

The following species is named in honor of Dr. Paulo Nogueira-Neto who has done so much to advance the knowledge of stingless bees, and on whose fazenda this carpenter bee was discovered nesting.

Xylocopa (Stenoxylocopa) nogueirai Hurd and Moure, new species
(Figures 1, 3–5)

MALE.—Length, 14–17 mm. Forewing including tegula, 13–15 mm. Head black, except broad, dorsally tapering, irregular yellow stripe situated on either side of face including at least lateral third of clypeus, contiguous with inner orbit, and terminating dorsally near posterior margin of vertex in a somewhat ovate spot; frequently as illustrated (fig. 1), but subject to some variation so that extent of median black facial stripe (stippled area) is sometimes narrower, especially on clypeus; supraclypeal area characteristically black, occasionally tinged with yellow or ferruginous; labrum yellow; mandibles black, except a large yellow maculation at base; scape black, rarely tinged in front with ferruginous; flagellar segments 2–13 black dorsally, paling to ferruginous below; metasomal sterna and apical tarsal segments including claws marked with piceous, body otherwise black. Wings lightly infuscated, weakly violaceous, feebly tinted with green. Vestiture chiefly pale, griseous, black pubescent on inner surfaces of middle and hind legs, also with a narrow strip of black pubescence on outer surface of hind tibia.

Eyes slightly more convergent above than below (112:113); maximum interorbital distance much less than length of eye (129:141); clypeus a little more than one-half as long as broad (65x113), somewhat longer than clypeocellar distance (65:57); interocellar distance scarcely greater than ocellorbital distance (29:27); orbitoccipital distance short, equal to ocelloccipital distance (27:27); interalveolar distance shorter than alveolorbital distance (30:33); first flagellar segment very short, slightly longer than combined length of succeeding two segments (22:10:11). Orbitoccipital area densely and confluently punctured, otherwise punctation very similar to other species.

Hind tibia, as seen from below, constricted near middle, shallowly and broadly sulcate along basal two-thirds, apical third elevated and partially traversed medially by a subcarinate, swollen ridge which extends basad and becomes adjacent to anterior ventral margin of tibia; pubescence on ventral surface of hind tibia not forming an extensive subapical patch of closely compacted hairs, at most with a small tuft of hairs near posterior ventral apex of tibia.

Genitalia as illustrated (figs. 3–5).

FEMALE.—Length, 14–19 mm. Forewing including tegula, 13–16 mm. Body black, except as follows: apical margins of metasomal sterna narrowly margined with piceous, middle and hind legs with inner surfaces of tibia and tarsi partly or largely ferruginous. Tegulae black. Wings heavily infuscated, brightly violaceous, effulgently blue-green apically. Vestiture entirely black.

Eyes slightly more convergent below than above

(141:142); maximum interorbital distance nearly as great as length of eye (160:164); clypeus scarcely more than one-half as long as broad (72x141), slightly shorter than clypeocellar distance (72:74); interocellar distance shorter than ocellorbital distance (35:40); orbitoccipital distance short, a little less than ocelloccipital distance (45:46); interalveolar distance greater than alveolorbital distance (46:40); first flagellar segment short, equal to combined length of succeeding two segments (27:13:14).

Holotype male, allotype female, and 47 paratypes (15 males, 32 females) were collected on the Fazenda Usina Estér, near Cosmópolis, São Paulo, Brazil during February 8–12, 1960 (Paulo Nogueira-Neto, J. S. Moure, and P. D. Hurd, Jr.). The holotype and allotype were deposited in the Museu Nacional, Quinta da Boa Vista, Rio de Janeiro, Brasil. Paratypes were placed in the collections of the U. S. National Museum, Washington, D. C., the private collection of Dr. Carlos Alberto Campos Seabra, Rio de Janeiro, as well as the collections of the authors.

This species is most closely related structurally to *Xylocopa artifex* Smith from which it differs most strikingly, as well as from the other species of the subgenus *Stenoxylocopa*, in the less strongly elevated vertex (fig. 1). The orbitoccipital distances in both sexes of *X. nogueirai* are much shorter (male, 27; female, 45) than those of *X. artifex* (male, 40; female, 65). In addition, the first flagellar segment of *X. nogueirai* is very short, approximately equal to the combined length of the succeeding two segments (male, 22:10:11; female, 27:13:14), while in *X. artifex* the first flagellar segment is considerably longer (male, 31:10:13; female, 35:12:15).

The interalveolar distance is equal in both sexes of *X. artifex* to the alveolorbital distance (male, 31:31; female, 43:43), but is shorter in the female of *X. nogueirai* (30:33) and longer in the male of that species (46:40). In the female of *X. nogueirai* the eyes are slightly more convergent below than above (141:142) while in the female of *X. artifex* the eyes converg much more above than below (137:143). The punctation of both species is remarkably similar, however, the punctures on the portion of the vertex lying above the upper extremities of the eyes are very crowded and confluent in the male of *X. nogueirai*. The heavily infuscated and brightly violaceous wings of the female *X. nogueirai* will immediately distinguish it from the more lightly infuscated, purplish-bronzed winged female of *X. artifex*.

Table 1.—Certain nest measurements (millimeters).

Nest No.	Internodal length (exterior)	Entrance position measured from:		Entrance diameters		Nest diameter (inside)
		(bottom)	(top)	(horiz.)	(vert.)	
1	340	120	220	6.5	7.0	9.0
2	240	82	158	6.5	8.0	10.0
3	170	50	120	7.0	8.0	9.8
4	286	106	180	7.0	8.0	10.0
5	310	50	260	7.0	9.0	9.0
6	186	82	104	6.5	8.0	10.1
7	335	147	188	7.0	9.0	9.5
8	356	185	171	7.0	8.5	10.0
9	198	94	104	7.0	9.0	8.5
10	360	135	225	7.5	7.0	9.0
11	324	116	208	8.0	11.5	10.5
12	378	171	207	7.0	9.0	10.5
13	256	152	104	6.5	10.0	6.5
14	249	121	128	7.5	7.5	10.0
15	361	136	225	7.5	10.1	11.5
16	155	75	80	7.0	9.0	8.0
17	232	82	150	7.0	9.0	9.0
18	302	64	238	8.0	9.0	9.0
19	325	153	172	7.0	7.5	9.5
20	380	180	200	7.5	8.0	10.0
21	393	176	217	7.0	7.5	10.5
22	320	127	193	7.0	7.5	7.0
23	327	82	245	6.5	7.0	7.0
24	290	105	185	7.0	9.0	9.0
25	298	116	182	7.0	10.0	13.0
26	400	171	229	7.0	9.0	10.0
27	375	23	352	6.5	9.5	10.5
28	230	115	115	7.0	9.0	10.0
29	400	285	115	6.5	6.8	8.5
30	348	124	224	7.0	7.5	9.5
Averages	304.13	120.83	183.33	7.02	8.50	9.48

Nests of *X. nogueirai* were found in four different stands of the same species of bamboo (*Bambusa* sp.) on the Fazenda Usina Estér, near Cosmópolis, São Paulo, Brasil during the period of February 8–12, 1960. The greatest number of nests were obtained on February 10 from an extensive row of bamboo clumps growing along an unsurfaced roadway near the fazenda headquarters (fig. 9). This stand of bamboo, approximately 10 meters in height, contained a large number of dead culms. The other few nests were located in bamboo clumps adjacent to the tracks of the fazenda railroad, in a small, heavily cut stand of bamboo growing in a gully, and in another roadside planting.

In all, 30 culms with the characteristic nest entranceway (fig. 10) were located and collected.

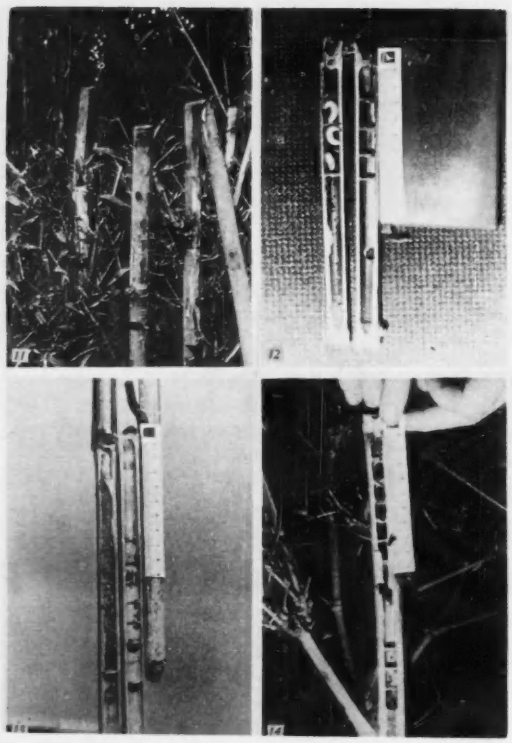


FIG. 11.—Nest entrance construction details. Note on the central culm the lower two attempts to bore an entrance before a successful entrance boring was achieved above.

FIG. 12.—Counterpart longitudinal sections of an internodal culm nest of *Xylocopa nogueirai* exhibiting the usual cell-length variation and the unused space at the top of the cavity.

FIG. 13.—Counterpart longitudinal sections of the internodal culm nest of *Xylocopa nogueirai* parasitized by *Cissites* (now in pupal stage, top end of nest).

FIG. 14.—Partly exposed internodal culm nest of *Xylocopa nogueirai* with two cell series. That above the entrance was parasitized by leucospid wasps.

These were subsequently split open longitudinally and, like the nests of other *Xylocopa* which are constructed in naturally hollow but internodally partitioned culms or stems, each nest whether new, reused, or old was confined to a single internodal cavity. As these culms were examined, each was assigned a nest number (1–30), certain measurements were recorded (table 1), and each was grouped according to the type of utilization (table 2).

Most of the nests occurred in culms that were completely dead; however, three of the nests (#μ, 28, 29) were situated in the dead upper parts of living culms. Two of these nests (#28, 29) were in dead internodal sections located immediately above the living part of the culms. The height of the nests above the ground, determined from the entrance, varied between 20 centimeters for the lowest to 5.4 meters for the highest. There is every likelihood that even higher nests existed above this level since it is difficult to see the small entrance at that height from the ground.

The altitudinal location of the nest is apparently determined at random. Within limits (table 1), neither the length of the internodal culm section housing the nest (range: 155–400 mm.) nor the inside nest diameter (range: 6.5–13.0 mm.) appears to be critical.

The majority of the nest entrances faced toward the exterior of the bamboo clumps. This type of orientation, which would seem to facilitate the departure and arrival of the bee, most likely occurred because the culms tend to lean outward so that an exteriorly placed entrance is somewhat protected from above. In view of this and since no entrances were found on the upper sides of the leaning culms, it may well be that the entrance is made intentionally on the least exposed side of the culm.

The entrances of all the nests studied, whether constructed this season or in past years, were somewhat longer than wide (fig. 10) and beveled so that the opening is slightly larger exteriorly. The maximum exterior horizontal and vertical diameters are presented in table 1. In all but one nest (#13), the entrance opened into the hollow internodal section below the middle of the cavity (table 1). Sometimes, as for example nest #27, the entrance was situated very near the bottom of the cavity. The inside diameters of the nests, as measured at the level of the entrance, were variably proportional to the outside diameters. Accordingly, there was a great variation in the thickness of the internodal walls from nest to nest (range: 2.0–8.5 mm.).

Some aspects of nest construction were evident from the nests collected. A new nest constructed in the present season can be recognized externally by the fresh appearance of the entrance. Nests built in preceding years, as evidenced by a number of internal features (see below), invariably had weathered entrances even if reoccupied this sea-

son by *Xylocopa*. On the evidence of a newly started nest entrance (fig. 11), the bee assumes a vertical, head-upward position on the culm and with her mandibles rasps a longitudinally elongate basin on the culm surface. After penetrating the culm wall, approximately at the middle of the basin, she rasps and tears away until the entranceway will accomodate her. This then accounts for the somewhat longitudinally elongate entrance, as well as the variable entrance sizes.

The interior walls of all the nests occupied by *Xylocopa* had been or were in the process (nests #12, 29) of being cleaned of loose plant matter (new nests) or old nesting debris. With the exception of two nests (#18, 28) discussed later, the cell series were built above the entrance in the upper portion of the internodal cavity. Physically at least, this space appears to be less subject to the vicissitudes of the environment (e.g., rainfall) than the lower portion of the cavity.

Presumably after the cavity is cleaned, the construction and provisioning of the cell series is commenced. A transverse partition is built usually near, but at varying distances from, the top of the cavity (fig. 12). This partition is apparently necessary when the upper end of the cavity is not (or cannot be fashioned) in the desired shape. This and every subsequent partition that serves to separate the completed cells is similarly constructed. Each consists of a spirally formed disc of cemented wood raspings which, in all cases, is started on the wall of the cavity. The disclike partition, thickest peripherally (±0.9 mm.) is concave and very smooth on the side nearest the nest entrance. The other side, nearly flat, is unfinished and the spiral pattern of construction is clearly evident. The partition placed in front of the final cell in the series is similarly somewhat concave but does not have the same smoothed surface as the partitions between or at the beginning of the cell series. This difference may be due to the fact that eventually the head of the pupa comes to lie in contact with the smoothed concave surface. Thus the proper orientation of the pupa for emergence from the nest may require the more perfectly made concave partition.

The virtually cylindrical cell walls, unlike the barrel-shaped cells of some species of *Xylocopa*, suggest that the raspings used to form the cell partitions are uniformly removed from the walls of the cavity. The cell walls were unlined and were without any trace of wax.

While the majority of the cells varied in length between 13 mm. and 15 mm., one cell was as short as 11 mm. and the longest cell 25 mm. (Note the variation in cell length in fig. 12). Occasionally, one of the cells in a series was sealed off unprovisioned. It may be, as observed in one such cell, that this occurs when the concave surface of a partition is poorly formed. The average number of cells in a completed nest was five. One nest (#26) originally had seven cells in the completed series (fig. 13) and only two survived the depredation of a *Cissites* larva.

Table 2.—Nesting culms grouped according to the type of utilization.

Nature of Use	Number of Nests	Nest No. (see table 1)
Inhabited Nests		
By *Xylocopa:*		
a) rearing of young	12[a]	1, 3–5, 10, 14, 18, 20, 24–26, 28
b) new construction	2	12, 29
c) congregated adults	6	6, 9, 11, 15, 19, 30
By other organisms:		
a) aculeate wasps	4[a]	5, 8, 17, 21
b) camponotine ant	1	2
c) lycosid spider	1	27
Uninhabited Nests		
Past appropriation:		
a) mud traces (wasps?)	3	16, 22,23
b) empty cells (*Euglossa?*)	1	7
c) no evidence	1	13

[a]One nest (#5) was both inhabited by *Xylocopa* and currently appropriated, see text for detail.

Twenty of the thirty nests were inhabited by *Xylocopa* (table 2), one of which (nest #5) con-

The sex ratio in the completed nests studied with pupae was 1.2 males to 1 female. The random occurrence of the male and female pupae within the examined cell series suggests that their sequence in any cell series is merely determined by chance. Some series, for example, had alternately male and female pupae, while others had some alternate as well as adjacent male or female pupae. The initial cell or the final cell in different cell series did not always have the same sex. None of the cell series contained all male or all female pupae. The provisioned cells contained a strongly scented pollen mass. The floral source of the pollen and nectar was not determined.

tained in the upper part, above a newly completed cell series of *Xylocopa*, a parasitized and psocid-infested cell series of an unemerged and still undetermined aculeate wasp. These two cell series were separated by a 6-mm.-thick mud plug, presumably made by the female wasp at the completion of her last cell. The side of this plug, nearest the nest entrance and against which the head of the first pupa (male) of the *Xylocopa* cell series rested, had been concavely fashioned. Whether this was accomplished by the wasp at the closure of her cell series or by the female *Xylocopa* at the initiation of her cell series is not certain. The other 10 nests, all previously used by the *Xylocopa*, were either currently appropriated (6 nests) or were without inhabitants (5 nests).

Of the currently appropriated nests, three (#8, 17, 21) contained completed cell series of the same wasp already mentioned, another housed the newly founded nest (#2) of a camponotine queen ant, and the last nest (#27), in addition to containing an old emerged cell series of a wasp, served as the dwelling of a lycosid spider. Four of the five currently uninhabited nests had traces of mud (nests #16, 22, 23) or old, emerged, resinous-coated cells (#7) suggesting past appropriated use by a bee of the genus *Euglossa*. Only one of the uninhabited nests (#13) lacked any evidence of recent occupancy.

In those nests currently occupied by *Xylocopa*, six (#6, 9, 11, 15, 19, 30) contained only adult bees: 3 males and 3 females, 2 males and 2 females, 2 males and 2 females, 2 males and 7 females, 1 male and 1 female, and 3 males and 2 females, respectively. These bees, as judged by their fresh appearance, their unfrayed wings, and the unworn mandibles of the females, had apparently emerged recently. It seems likely that they were either congregated in these old nests because of the inclement weather or were already commencing hibernation. The bees, however, were not in a torpid state and were capable of flight when the nest was split open. Another two nests, one being refurbished (nest #29) and the other with a partly provisioned first cell (nest #12), were each occupied by a single female, both of which were in worn condition (second nests?).

The remaining twelve nests (#1, 3–5, 10, 14, 18, 20, 24–26, 28) housed cell series of young *Xylocopa* ranging from the egg[4] in nest #18 to the darkly pigmented pupae of nests #24 and #26. All of these nests contained in the antechamber at least one adult female and in some nests there were both males and females (nests #1, 24, 26) or another female (nest #18). In these latter nests, excepting nest #18, it appears that the founding female was no longer associated with her nest, since the bees occupying the antechamber were in fresh condition. In contrast, the solitary females in nests #3–5, 10, 14, 20, 25, and 28 all possessed worn mandibles and wings. On this basis, these females probably were the nest founders. The two females in nest #18 likewise appeared to be founding females and since there were two cell series, one above and the other below the entrance, they may have been sharing the same nest cavity. However, one other nest (#28), with two similarly disposed cell series, contained only one female in the antechamber.

Four nests with cell series of *Xylocopa* were either parasitized or contaminated with mold. One of these nests (#26), which originally had seven completed cells, contained at the top of the cavity a cell with a pupa of the genus *Cissites* (Meloidae). Evidently, while in its larval stage, this beetle had destroyed five cells in the process of consuming the contents of these cells. The two undamaged cells, nearest the entrance of the nest, were each occupied by a male *Xylocopa* pupa at the time the nest was collected. Although the essentially Pantropical genus *Cissites* has been previously recorded from four nests of New World *Xylocopa* (Hurd, 1958: 372), this is the first time it has been found in a nest housed in bamboo. As may be seen (fig. 13), the plug of this *Cissites* pupal cell is much thicker than the *Xylocopa* cell partitions, it nonetheless is considerably shorter than the elongate plugs illustrated by Strand (1912: 264) and Hurd (1958: 369). Unlike those also, this *Cissites* pupal cell was not excavated beyond the upper terminus of the nest cavity.

The other parasitized nest (#1), shown in figure 14, had 10 adults (2 males, 8 females) of an undescribed species of *Leucospis* which were apparently ready to leave the nest. These wasps had destroyed, in the course of larval feeding, the entire *Xylocopa* cell series. Even though several species of the family Leucospidae are regularly parasitic in the nests of bees, this is the first time that one of these wasps has been found in a nest of *Xylocopa*. Other families of the superfamily Chalcidoidea which have been reported as parasitic in the nests of *Xylocopa* include Chalcididae (Giraud, 1863: 1306; Schulz, 1911: 396; Brauns, 1913: 118; Jacobson, 1927: 101), Encyrtidae (Horne, 1872: 179; Kannan, 1925: xiii; Maa, 1940: 568), and Torymidae (Davidson, 1893: 151).

Mold had contaminated one of the two cells in nest #24 and had killed the half-grown larva. The other cell, containing a pigmented female pupa, was not affected. The lowermost cell in the cell series located above the entrance in nest #18 held a moldy, half-matured larva which

[4]Although three provisioned cells in a series with very young larvae were carefully examined by dissecting the pollen masses and subsequently immersing them in water, no eggs were located. The cell walls, including the partitions, were also without adhering eggs. Possibly no eggs had been laid in these cells.

though still living was quite flaccid. The larvae in the four cells above it were normal in appearance.

It seems appropriate to record here some additional information relating to the nesting habits of the subgenus *Stenoxylocopa*. Historically, Schrottky (1904: 347) was the first to comment on the nest of *Xylocopa artifex* Smith (given as *X. colona* Lepeletier, subsequently corrected by Brèthes, 1916: 411). Schrottky noted merely that the nest "Anlage" of this species that he had observed earlier in Brazil was similar to that of *X. frontalis* (Olivier). He found the species to be uncommon in Paraguay and on occasion could be seen at the flowers of *Solanum*. In Brazil, Schrottky (1902: 468) stated that the females were encountered on the same flowers with *X. brasilianorum* (Linnaeus), viz., p. 466, *Solanum balbisii*, *S. paniculatum*, *S. atropurpureum*, *Leonurus sibiricus*, *Crotalaria paulina*, *Cassia bicapsularis*, *C. splendida*, and "etc." The males he had collected on the flowers of *Baccharis dracunculifolia* at São Paulo (Ipiranga), and *Tecoma ipê* at Jundiaí, S. P., Brasil.

The next nest of this species, also erroneously identified as *X. colona* Lepeletier, was briefly reported by Strand (1912: 267) from Asunción, Paraguay. The nest had been constructed in the hollow cavity of a dead stem questionably identified as *Guadua* that was supporting a rose bush in the garden of the U. S. Consul. The nesting cavity measured 110 mm. in length, 10 mm. in breadth and the entrance opened into the middle of the cavity. On the day the nest was examined, March 22, 1905, the uppermost part of the cavity contained "Wachs und Pollen" and adhering to the nest entrance was also a little wax. This is the only record to our knowledge of wax being reported in a *Xylocopa* nest.

Bertoni (1918: 219) stated that his brother had discovered a nest of *X. artifex* in a culm of bamboo determined as *Merostachys clausseni* Munro. In the short description of the nest it is not clear whether the culm was living or dead. The nest had two cells above the entrance and four below it. The cell partitions, approximately 15 mm. apart, were made of wood rasped from the interior of the same culm. The entrance, acircular in outline, measured 8 mm. in diameter, presumably along the horizontal axis. The cells contained only young adults. The nest most likely had been collected in Puerto Bertoni, Paraguay.

The most recently described nest of *X. artifex* is that by Moure (1942: 301). This nest, which had been collected during December of 1940 in São Paulo, S. P., Brasil, by R. L. Araujo, was situated in a dead bamboo culm measuring approximately 290 mm. in length and had an external diameter of 19 mm. The entrance, 8.3 mm. in diameter, opened into an antechamber of some 60 mm. in length, above and below which were cell series containing pupae (four males and five females). The eight cells in one series each measured 14.7 mm. (±0.2 mm.) in length and the seven cells in the other series were each approximately 14 mm. (±0.15 mm.) in length.

This is the largest number of cells (15) thus far discovered within a single internodal culm section inhabited by a species of the subgenus *Stenoxylocopa*. As in some other nests discussed above, it is possible that two females may have shared the cavity during the construction of the two cell series. It is also possible that these cell series may have been initiated at different times by the same or another female. However, since pupae were found in both cell series, they probably were built simultaneously.

The question of two separate cell series in one culm nest presents an interesting possibility for further investigation. A study of mutual sharing by one or more females of the same nest cavity, reported several times for *Xylocopa*, could contribute importantly to the knowledge of social development in bees.

While attending the meetings of the Primer Congreso Sudamericano de Zoología held in October of 1959 at La Plata, Argentina, Dr. Alejandro A. Ogloblin presented us with an old nest of *X. artifex* which had been collected in Buenos Aires during the previous nesting season. The nest had been made in a dead and very short (146 mm.) culm section of *Arundo donax* Linnaeus. At the time the nest was collected it contained four completed cells above the entrance and two below it. Both cell series, each with shriveled larvae and partly consumed pollen masses, were initiated by a transverse partition situated near either extremity of the cavity. The length of each cell was remarkably uniform and measured approximately 14 mm. The cells were virtually cylindrical and lacked the barrel-shaped appearance of certain other groups of *Xylocopa*. The inside culm diameter was 10.5 mm. The entrance, situated approximately 55 mm. from the bottom of the culm, had been largely destroyed by an earlier examination of the nest. In the antechamber between the cell series were two adult females, and judging by the criteria discussed above, they could well have been the founding females of the respective cell series. It is especially interesting that at the time of collection they were sharing an antechamber space of only 26 mm. in length.

Two nests of *X. artifex*, which had been collected by K. Lenko in March of 1957 at Barueri, São Paulo, Brazil, were presented to us by Dr. C. A. Campos Seabra, of Rio de Janeiro, for study. Both nests had been constructed in the dead culm sections of unidentified bamboo. One of these nests, collected on March 13, contained a female which, to judge by the appearance of the entrance, had only commenced construction. The walls within the 253-mm.-long internodal

section had been evenly rasped to a distance of 80 mm. above the entrance. In the lower end of the cavity there was an accumulation of sawdust about 10 mm. in depth. Otherwise the interior of the culm was unaltered and no cell series had been started. The entrance, longest longitudinally, measured 8 x 9.5 mm. and was situated 64 mm. above the lower internodal partition. The inside diameter of the culm at the level of the entrance measured 10.5 mm.

The other nest from Barueri contained at the time of collection, March 25, three females all in fresh condition. The nest was very old in appearance and exhibited a well-seasoned entrance in addition to remnants of old cell partitions. On this evidence it seems likely that these bees were using the old nest for resting purposes. The internodal culm length measured 210 mm., the inside diameter at the level of the entrance was 12.5 mm., the entrance was situated 97 mm. from the lower internodal partition, and the entrance, very nearly circular in outline, measured 9 mm. (horizontally) and 10 mm. (vertically).

Four hibernating nests of *X. artifex* were discovered by us on September 16, 1959, at Bariguí, near Curitiba, Paraná, Brazil. These nests are of particular interest since the internodal culms of the bamboo (*Chusquea bambusoidea* H.K.) in which the nests had been constructed at least during the last nesting season were still alive. No difference in appearance between these culms and the nearby alive ones without nests could be detected. Only two other species of *Xylocopa*, *X. aestuans* (Linnaeus) (Dover, 1924) and *X. sicheli* Vachal (Brauns, 1913), have been found nesting in a living plant, although a number of species are known to nest regularly in the dead parts of living plants. One of these Bariguí nests, which contained four bees of each sex, measured 445 mm. in length and had a variable inside diameter of 12–15 mm. Two entrances, the lower located at 65 mm. above the internodal partition and the higher at 202 mm. above this point (137 mm. between entrances), opened into the same cavity. The other three nests were shorter in length (275, 310, and 340 mm.), had the same variation in inside diameter, and each had a single entrance situated at 95, 110, 65 mm., respectively. Each of these latter nests contained: 1 male and 2 females, 2 males and 1 female, and 4 males and 6 females, respectively. The nest entrances of the four Bariguí nests measured in millimeters, horizontal diameter recorded first, were: 7.5 x 8.5 (top entrance), 7.5 x 9.0 (bottom entrance), 6.8 x 7.0, 9.0 x 10.5, and 7.5 x 9.0. The culm walls of all these nests were quite thin (1.5 mm.), in fact the thinnest walls of all the nests of this subgenus so far studied by us.

After the completion of this study two additional nesting sites in the dead culms of bamboo, one of *Xylocopa artifex* and one of *X. nogueirai*, were located in Brasil. The latter species was discovered on April 30, 1960 with the help of Dr. G. M. de Oliveira Castro nesting in a small roadside clump of bamboo (*Bambusa*) near the Lagoa Santa Field Station (Entidade do Instituto Oswaldo Cruz) in Minas Gerais. All but one of the nests investigated contained only adult bees, males and females, in both worn and unworn condition. In view of this and the presence of cell remnants, these bees, although not in a torpid state, were probably commencing hibernation. Nest construction, as evidenced by the examined nests did not differ significantly from those of the same species studied at the fazenda of Dr. Paulo Nogueira-Neto reported above. It is of interest, however, that one nest contained three provisioned cells and a worn female (mandibles and wings) in the antechamber. Since an examination of the cell provisions failed to reveal eggs or larvae, it is believed that the nest had been constructed during the preceding summer rather than late in the fall season as its contents seemed to suggest.

A number of old nests of *Xylocopa artifex* were discovered with the assistance of Dr. C. A. Campos Seabra and Senhor Moracir Alvarenga in some landscaped clumps of an unidentified bamboo growing in Bom Retiro, Floresta de Tijuca, in Rio de Janeiro on May 3, 1960. Of the five nests collected for study, two had been appropriated, two contained adult bees of both sexes in unworn condition, and one nest was uninhabited. The appropriated nests served respectively, as dwellings for an ant colony and a spider. The nests exhibited construction details similar to those described above for the same species at Barueri, São Paulo.

It seems almost a certainty that the other species of the subgenus *Stenoxylocopa* will be found nesting in the hollow cavities of internodally partitioned stems, especially the culms of bamboo. The curiously modified mandibles of these females, which by virtue of the greatly widened and obliquely truncated inner apical tooth, appear to be particularly well suited for entrance boring and subsequent rasping of the interior culm walls. It seems further likely that this specialization precludes nest construction in solid wood and, accordingly, their distribution is to a large degree determined, under natural conditions, by the geographic availability of the hollow culm habitat.

REFERENCES CITED

Bertoni, A. de Winkelried. 1918. Notas entomológicas (biológicas y sistematicas). An. Cient. Paraguayos, ser. 2, núm. 3: 219–31.

Brauns, H. 1913. Biologie südafrikanischer Apiden. Zeitschr. wiss. Insektenbiol. 9: 116–20, 190–3.

Brèthes, J. 1916. Le genre "Xylocopa" Latreille dans la République Argentine. Physis 2: 407–21, 1 text fig.

Cockerell, T. D. A. 1904. Descriptions and records of bees. Ann. Mag. Nat. Hist. (7) 14: 21–30.

Davidson, A. 1893. The nest and parasites of *Xylocopa orpifex* Smith. Ent. News 4: 151–3.
Dover, C. 1924. Some observations on the bionomics of *Xylocopa aestuans* Linn. (Apidae). Trans. Ent. Soc. London 1924: 144–50, 1 text fig.
Dusmet y Alonso, J. M. 1924. Las "Xylocopa" (Hymen. Apidae) en las colecciones de Madrid. Trabajos Mus. Nac. Cienc. Nat. Madrid, ser. zóol., núm. 49: 5–58.
Enderlein, G. 1913. Zur Kenntnis des Xylocopen Südamerikas und über einen zwitter von *Xylocopa ordinaria*. Arch. Naturgesch. (A) 79(2): 156–70.
Friese, H. 1903. Neue Arten der Bienengattung *Xylocopa* Latr. aus der neotropischen und orientalischen Region. Zeitschr. Hymen. Dipt. 3: 202–8.
Giraud, J. E. 1863. Note sur quelques Hyménoptères Très rares découverts en Autriche, et description d'un Chalciden nouveau (*Dirrhinus imperialis*). Verh. k. k. Zool.-Bot. Gesellsch. Wien 13: 1306–12.
Hoffmann, W. E. 1938. The nidification of the bamboo bee, *Xylocopa dissimilis* Lepel. (Hymenoptera: Xylocopidae). Lingnan Sci. Jour. 17: 87–91, 2 figs.
Horne, C. 1870. Notes on the habits of some hymenopterous insects from the Northwest Provinces of India; with an appendix, containing descriptions of some new species of Apidae and Vespidae collected by Mr. Horne: by Frederick Smith of the British Museum. Trans. Zool. Soc. London 1872: 161–96, pls. XIX–XXII.
Hurd, P. D., Jr. 1958. Observations on the nesting habits of some New World carpenter bees with remarks on their importance in the problem of species formation (Hymenoptera: Apoidea). Ann. Ent. Soc. Amer. 51: 365–75, 5 figs.
Jacobson, E. 1927. Fauna sumatrensis (Beitrag nr. 53): Xylocopinae (Hym.). Biol. Suppl. Ent. 16: 93–103.
Kannan, K., *in* Poulton, E. B. 1925. Confirmation by Dr. Kunhi Kannan in S. India of Dr. V. G. L. van Someren's observations on *Hyperechia* and *Xylocopa* at Nairobi. Trans. Ent. Soc. London 1924: xii-xiii.
Lepeletier de Saint-Fargeau, M. le Compte Amédée Louis Michel. 1841. Histoire naturelle des insectes. Hyménoptères. Suites à Buffon. Paris, Roret 2: 1–680.
Maa, T. (Maa Tsing-chao). 1940. *Xylocopa* orientalia critica (Hymen.). III. Subgenus *Platynopoda* Westw. Lingnan Sci. Jour. 19: 565–75, 3 text figs.
1946. *Xylocopa* orientalia critica (Hymen.). V. Subgenus *Biluna* Maa. Biol. Bull. Fukien Univ., Foochow 5 [?1947]: 67–92, text figs. 10 (maps), 11.
Moure, P. J., C.M.F. 1942. Abelhas de Salobra (Hym. Apoidea). Papéis Avulsos Dept. Zool., Secretaria Agric., São Paulo 2: 291–321.
Schrottky, C. 1902. Ensaio sôbre as abelhas solitárias do Brasil. Rev. Mus. Paulista 5: 330–613, pls. XII–XVI, 6 figs.
1904. Beitrag zur Kenntnis einiger südamerikanischer Hymenopteren. Allgem. Zeitschr. Ent. 9: 344–9.
Schulz, W. A. 1911. Stechen tropische *Chalcis*-Arten auch Bienenimagines an? Zeitschr. wiss. Insektenbiol. 7: 396.
Smith, F. 1874. Monograph of the genus *Xylocopa*, Latr. Trans. Ent. Soc. London 1874: 247–302.
Strand, E. 1912. Beiträge zur Kenntnis der Hymenopterenfauna von Paraguay auf Grund der Sammlungen und Beobachtungen von Prof. J. D. Anisits.—X. Zool. Jahrb. Abt. Syst. 33: 257–346, 2 pls., 15 text figs.

EFFECT OF DIETARY CHOLESTEROL ON HOUSE FLY REPRODUCTION[1]

R. E. MONROE

Entomology Research Division, Agr. Res. Serv., U.S.D.A., Beltsville, Md.

ABSTRACT

The effect of cholesterol deficiency on survival and reproduction of the adult house fly (*Musca domestica* L.) was investigated. The preparation and composition of the synthetic diet used in these studies are reported. Although a cholesterol deficiency had no appreciable effect on adult survival or total egg production, it caused nearly an 80% reduction in egg hatch. Only about half the eggs that hatched from the flies fed the sterol-deficient diet produced adults when reared on a larval medium containing sufficient sterols to support growth. Of the various cholesterol concentrations tested, 0.1% gave the highest cumulative hatch (92%) and a total viable egg production about 30% greater than that found for the control diet (sucrose: defatted dry milk solids 1:1).

The adult house fly, *Musca domestica* L., requires a dietary source of sterol for the sustained production of viable eggs (Monroe 1959). Although omission of the sterol from the diet had little effect on ovarian growth or total egg production, it caused an appreciable decrease in hatch.

This paper presents a more detailed account of the effects of a sterol deficiency on the reproductive processes of the house fly, and reports the preparation and composition of a synthetic diet for this insect.

[1]Accepted for publication April 18, 1960. Presented at the annual meeting of the Entomological Society of America, Detroit, Mich., November 30, 1959.

MATERIALS AND METHODS

House fly larvae were reared by the CSMA procedure (1955) and the puparia separated from the medium and thoroughly randomized. Groups of 600 puparia were placed in beakers and the flies allowed to emerge in screen cages. To prevent the flies from having access to the puparial cases, which have been found to contain sterols, the beakers were covered with paper cones. The flies were held at a temperature of 28° ± 2° C. and

a relative humidity of approximately 50% throughout the experimental period.

The synthetic diet fed to the adult flies was composed of the following constituents:[2]

	Parts
Vitamin free casein	47.0
Sucrose	47.0
Sodium oleate	2.0
Salts[3]	4.0
Yeast ribose nucleic acid	0.1
Cholesterol (final concentration 0.1%)	
B-Vitamin mixture	

The vitamin mixture[4] was similar to that reported by Rasso and Fraenkel (1954), with the concentrations adjusted for a dry diet:

	Mg./100 gm. diet
Thiamine hydrochloride	50.0
Riboflavin	25.0
Nicotinic acid	100.0
Pantothenic acid	50.0
Pyridoxine hydrochloride	25.0
Choline chloride	1,000.0
Inositol	500.0
Folic acid	5.0
Biotin	1.0

The casein, sucrose, sodium oleate, salts, and ribose nucleic acid were ball-milled for 4 to 5 hours. The cholesterol, when present, was added as a dichloromethane solution and the mixture stirred occasionally while the solvent evaporated.

The B-vitamins were dissolved in distilled water with the addition of 2 to 4 drops of concentrated ammonium hydroxide. Ten ml. of the vitamin and zinc chloride solution was then added to 100 gm. of the diet and the mixture ground in a mortar. The diet was then dried at room temperature and held at −30° C. until used.

Table 1.—Mean percent survival of male and female house flies held on control and synthetic diets for 22 days.

Diet	Females	Males
Control (milk-sucrose 1:1)	83	6
Synthetic:		
With cholesterol	82	5
Without cholesterol	85	7
Without and then with cholesterol	85	4

The diets were placed in the cages when the first flies began to emerge, and subsequently changed every third day. Distilled water was provided in waxed cups with a thin piece of styrofoam floating on the surface to provide greater accessibility and to prevent drowning. To prevent cannibalism, which may serve as a source of nutrients (Ascher and Levinson 1956), the dead flies were removed twice daily.

Table 2.—Effect of cholesterol deficiency on egg production and hatch.

Diet	Ml. of eggs per 100 females		Cumulative percent hatch
	Total	Viable	
Control	4.8	4.7	98
Synthetic:			
With cholesterol	6.6	6.1	92
Without cholesterol	6.3	1.3	21

Table 3.—Effect of cholesterol deficiency on egg hatch and adult emergence.

Egg Collection No.	Diet with cholesterol		Diet without cholesterol	
	% Hatch	% Adult emergence	% Hatch	% Adult emergence
1	96	98	77	52
2	93	95	70	24
3	95	88	11	4
4	93	96	5	3
5	90	74	2	0

To stimulate oviposition, muslin bags containing absorbent cotton saturated with an ammonium carbonate solution were placed in Petri dishes inside the cages. The eggs were collected on the sixth day and thereafter on alternate days until nine collections had been made. The flies were allowed to oviposit for approximately 7 hours. The eggs were transferred to a centrifuge tube containing water and

Table 4.—Effect of cholesterol concentration on egg production and hatch.

Cholesterol concentration (%)	Ml. of eggs per 100 females		Cumulative percent hatch
	Total	Viable	
0.05	5.4	4.8	89
.01	6.0	4.4	73
.005	7.0	3.4	49
.001	6.4	2.4	38

[2]The vitamin-free casein, sodium oleate, salts, and nucleic acid were obtained from Nutritional Biochemicals Corp., Cleveland, Ohio; the sucrose was obtained locally in the form of granulated cane sugar; and the cholesterol was a purified grade received from California Foundation for Biochemical Research, Los Angeles, Calif.

[3]Modification of the Osborne-Mendel salt mixture (Wesson 1932) plus 0.02% of zinc chloride (Fraenkel 1958).

[4]The inositol was obtained from Difco Laboratories, Inc., Detroit, Mich.; the remaining vitamins from Nutritional Biochemicals Corp., Cleveland, Ohio.

thoroughly mixed. Duplicate aliquots of approximately 200 eggs (0.02 ml.) from each cage were placed in Petri dishes containing water-saturated filter paper[5]. Additional duplicate aliquots were placed in pint jars containing CSMA medium. The remaining eggs were centrifuged for 10 minutes at approximately 1,000 r.p.m., and the total volume measured in milliliters. After 24 hours the eggs in the Petri dishes were examined and the hatch determined. The number of adults emerging from the CSMA medium were counted and recorded.

The synthetic diet was tested in triplicate in the following ways: Flies fed on the diet with or without cholesterol, and flies fed on the diet without cholesterol for the first four egg collections and then given this diet with cholesterol for the remainder of the test. For this series of tests the control flies were fed on this laboratory's standard diet of sucrose-defatted dry milk solids (1:1). This diet contains 0.01% Δ^5-sterols and trace amounts of $\Delta^{5,7}$-sterols, as determined by a modified Liebermann-Burchard test (Moore and Baumann 1952) based on cholesterol and 7-dehydrocholesterol as standards.

To determine the concentration of cholesterol necessary for normal reproduction, duplicate tests were conducted with the following concentrations in the synthetic diet: 0.05, 0.01, 0.005, and 0.001%. Flies fed on the synthetic diet containing 0.1% cholesterol and without cholesterol served as controls.

[5]Reeve-Angel No. 230, 9 cm. diameter.

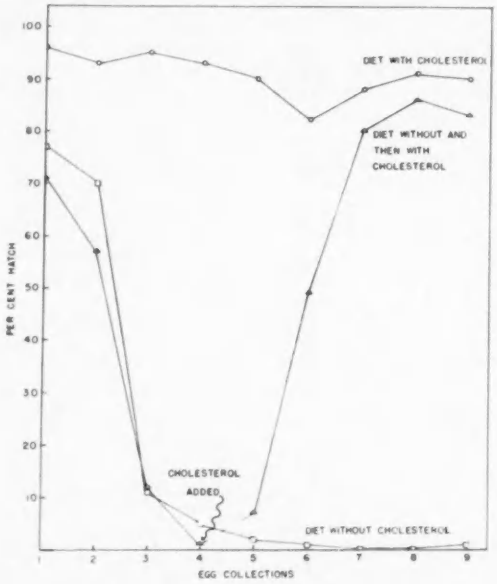


FIG. 1.—Effect of dietary cholesterol deficiency on egg hatch.

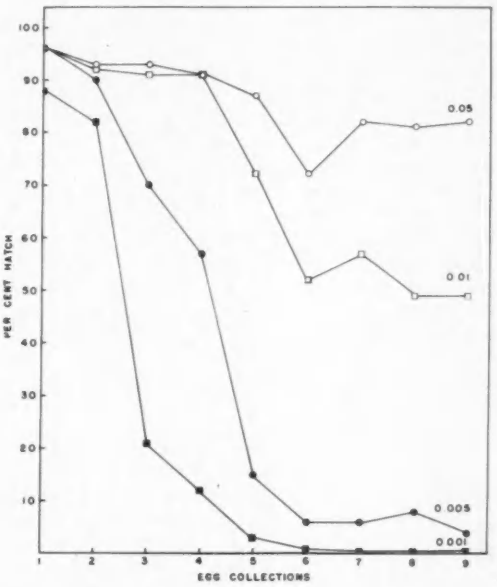


FIG. 2.—Effect of varying concentrations of dietary cholesterol on egg hatch.

RESULTS

The mean percent survival of the male and female flies at the end of the 22-day experimental period is given in table 1. At this time most of the female flies were still living, with a range of 82% to 85% for all diets. However, the male survival was only from 4% to 7%.

The total and viable egg production and the cumulative hatch are summarized in table 2. The flies fed on the synthetic diet with or without cholesterol both produced more eggs than those on the control diet. The cumulative percent hatch for both the control and the synthetic diet with cholesterol was greater than 90%, but only about 21% of the eggs hatched from the cholesterol-deficient diet.

The effect of the sterol deficiency is shown in figure 1. For both the control diet and the synthetic diet plus cholesterol the egg hatch ranged between 82% and 97%. When cholesterol was omitted from the diet, the hatch was initially lower and decreased rapidly until by the fourth collection it approached zero. If at this time the flies were given the diet plus cholesterol, the hatch increased progressively until by the ninth collection it was similar to the controls. When the larvae were reared through to adults on the CSMA medium, only about 50% of those

that hatched from the sterol-deficient diet produced adults, as compared with 91% from the diet containing cholesterol (table 3).

When the concentration of cholesterol was varied, the hatch was found to decrease with sterol concentration (table 4, fig. 2). Although there was variation in the total egg production, the flies fed on the synthetic diet plus 0.01% and 0.05% cholesterol produced approximately the same quantity of viable eggs as those on the sucrose-defatted milk diet, but considerably less than that found for this diet plus 0.1% cholesterol (tables 2 and 4). The viable egg production, the cumulative hatch, and the general pattern of decreasing egg viability for the synthetic diet plus 0.001% cholesterol very closely approximated that found for the sterol-deficient diet.

At the end of the experimental period (22 days) 3-day-old male flies fed on the standard diet were placed in the cages with the surviving females fed on the sterol-deficient diet. After 2 days eggs were again collected from the flies and the hatch determined. This procedure did not cause an increase in egg hatch.

DISCUSSION

Although dietary cholesterol is necessary for the production of viable eggs, the quantity of eggs oviposited is not markedly affected by a cholesterol deficiency. Apparently cholesterol is necessary for growth of the embryo but not for ovarian development. However, a cholesterol-deficient diet must also affect ovarian growth in some manner, because eggs collected from these flies were usually small, and often deformed or oval in shape. This phenomenon is not yet clearly understood.

Fifty percent of the larvae hatching from eggs oviposited by flies fed on the cholesterol-deficient diet did not survive to become adults, even though they were placed in a medium containing sufficient naturally occurring sterols to support growth. This suggests that some of these larvae must be in a weakened condition. Observations made on these larvae confirmed this. Many died either as partially formed embryos or fully developed larvae in the egg, or as partially emerged larvae.

Since hatch on the cholesterol-deficient diet did not approach zero until about the fourth egg collection, apparently the female fly must transfer stored sterols to at least the first groups of eggs produced. This is substantiated by previous work which has shown that, although the adult house fly contains an appreciable amount of both Δ^5 and $\Delta^{5,7}$—sterols (Monroe, unpublished data), it lacks the biochemical mechanism for sterol biosynthesis (Robbins et al. 1960), indicating that storage must be the source of these sterols. When the concentration of cholesterol was varied, the decrease in egg hatch on succeeding collections was approximately proportional to the concentration of sterol. Thus the storage was depleted more slowly at the higher concentration.

The highest cumulative hatch was found for the control diet, although the flies fed on the synthetic diet plus 0.1% cholesterol produced approximately 30% more viable eggs, and the diets containing 0.05% and 0.01% about equaled the control diet in viable egg production. The lesser cumulative hatch from the synthetic diets containing as much or more sterol than the control diet was probably caused by accelerated ovarian growth due to the higher nutritional value. This resulted in a more rapid oogenesis and required an increased cholesterol concentration to maintain the level that was necessary for egg viability.

These results stress that in evaluating the effects of certain nutrients in insect reproduction, merely measuring the length of ovaries or counting the eggs is inadequate. Only from adult survival, total egg production, egg hatch, and larval viability can a true picture of what is actually occurring be determined.

REFERENCES CITED

Ascher, K. R. S., and **Z. H. Levinson.** 1956. The influence of protein addition to the larval diet on oviposition of the house fly. Riv. Parassitol. **17**: 217–22.

Chemical Specialty Manufacturers Association. 1955. Peet-Grady method. Soap and Sanitary Chem. Blue Book, pp. 249–50, 267.

Fraenkel, G. S. 1958. The effect of zinc and potassium in the nutrition of *Tenebrio molitor*, with observations on the expression of a carnitine deficiency. Jour. Nutrition 65: 361–95.

Monroe, R. E. 1959. Role of cholesterol in house fly reproduction. Nature 184: 1513.

Moore, P. R., and **C. A. Baumann.** 1952. Skin sterols. I. Colorimetric determination of cholesterol and other sterols in skin. Jour. Biol. Chem. 195: 615–22.

Rasso, S. C., and **G. Fraenkel.** 1954. The food requirements of the adult female blow fly, *Phormia regina* (Meigen), in relation to ovarian development. Ann. Ent. Soc. America 47: 636–45.

Robbins, W. E., J. N. Kaplanis, S. J. Louloudes, and **R. E. Monroe.** 1960. Utilization of 1-C^{14}-acetate in lipid synthesis by adult house flies. Ann. Ent. Soc. America 53: 128–9.

Wesson, L. G. 1932. A modification of the Osborne-Mendel salt mixture containing only inorganic constituents. Science 75: 339–40.

ERRATUM

In volume 53 (Sept. 1960), page 582, column 2, line 14:
change *S. menkei* L. Smith to read *S. stangei* L. Smith.

NEW TERMITOPHILOUS STAPHYLINIDAE OF ZOOGEOGRAPHIC SIGNIFICANCE (COLEOPTERA)[1]

CHARLES H. SEEVERS[2]
Roosevelt University, Chicago, Illinois

ABSTRACT

Zoogeographical and evolutionary considerations and host relationships of termitophiles in the aleocharine tribe Corotocini (subtribes Corotocina and Termitogastrina), and of the termitophilous subfamily Trichopseniinae, are discussed. New taxa in the Corotocina are: *Thyreoxenus* **mexicanus,** from Campeche, whose host probably is a *Nasutitermes*, and **SPIRACHTHODES,** type *S.* **madecassus,** found with *Nasutitermes kauderianus* in Madagascar. This latter is the first Old-World genus with exudatory abdominal appendages, a remarkable adaptive feature shared only with *Spirachtha* Schiödte of Brazil and British Guiana. New species of Termitogastrina are: *Termitoplochus* **australiensis,** from a nest of *Tumulitermes apiocephalus* in Western Australia; *Idiogaster* **coatoni,** collected with an undescribed *Trinervitermes* in Northern Rhodesia; and *Protermitobia* **rhodesiae,** taken with *Cubitermes* sp. in Northern Rhodesia. The first known Ethiopian genus of Trichopseniinae is **TERMITONA,** type *T.* **congoensis,** from nest of *Schedorhinotermes lamanianus* in the Belgian Congo; its closest relative is *Schizelythron*, in Java. New synonymy: *Idiogaster* Wasmann, 1912 (= *Termitotima* Wasmann, 1916).

In 1853, Schiödte announced the discovery of *Spirachtha*, one of the most highly specialized beetles living in societies of social insects. Well adapted to the social life of Brazilian and British Guiana termites of the genus *Constrictotermes*, *Spirachtha* possesses three pairs of abdominal appendages that serve as exudatoria for elaboration of a secretion attractive to their hosts. For more than a century no counterpart of this genus has been reported in the Old World, and *Spirachtha* has been unique among adult termitophilous insects in having exudatory appendages. Recently, while examining a series of termites from the Stockholm Museum collected in Madagascar in 1911, Dr. Alfred E. Emerson found representatives of a genus closely allied to *Spirachtha*. This outstanding new Madagascan genus, *Spirachthodes*, and other termitophilous Staphylinidae of unusual zoogeographic interest are the subject of this paper.

Termite societies with their associated termitophiles are interspecies systems of considerable evolutionary and zoogeographic interest. In a systematic monograph on the world fauna of termitophilous Staphylinidae (Seevers 1957), I attempted to construct broad outlines of the evolutionary histories of several such interspecies systems. The 100-odd staphylinid genera involved in that study belong to more than a dozen independently evolved termitophile groups, of which a large majority are restricted to the tropical zone. Each group evidently stemmed from a single species adapted to social life; some groups have pantropical distributions and are probably very ancient, while others are restricted to either the American or Old World tropics and seem to be of more recent origin.

[1]Accepted for publication April 11, 1960. Research carried out during the tenure of a grant from the National Science Foundation.

[2]Research Associate, Chicago Natural History Museum.

ACKNOWLEDGEMENTS

For the privilege of studying the species described herein, I am indebted to W. G. H. Coaton (Division of Entomology, Department of Agriculture, Union of South Africa), Alfred E. Emerson (The University of Chicago), F. J. Gay and John Calaby (Commonwealth Scientific and Industrial Research Organization, Australia), E. M. Kruytzer (Natuurhistorisch Museum, Maastricht, The Netherlands), A. Reichensperger (Bad Gödesberg, Germany), and the authorities of the Stockholm Museum.

ZOOGEOGRAPHIC AND EVOLUTIONARY CONSIDERATIONS

1. *The Tribe Corotocini (Aleocharinae)*

The new Madagascan genus *Spirachthodes* and several new species of other genera belong to the pantropical tribe Corotocini, a group of 46 recorded genera. The evolution of the Corotocini was very closely linked to the evolution of the termite subfamily Nasutitermitinae (Seevers 1957). Evidence indicates that this association of beetles and termites began early in the history of the Nasutitermitinae, probably soon after their differentiation.

In several papers (1949, 1952, 1955), Dr. Alfred E. Emerson has postulated the general time and place of the origin of the Nasutitermitinae and the subsequent dispersal pattern for the subfamily. Emerson believes that the Nasutitermitinae originated in the American tropics in the Mesozoic, and that specialized genera with distinctive nasute soldiers (e.g., *Nasutitermes*) differentiated in the Americas and dispersed in pre-Tertiary time to the Old World tropics, probably by an Alaskan land connection. At present, the generalized Nasutitermitinae are restricted to South America while the derived nasute genera are pantropical, a distribution that probably existed before the Tertiary Period.

The zoogeography and host relationships of the staphylinid beetles support Emerson's conclusions very well. In the case of the Corotocini, the relatively generalized forms occur with the generalized nasutitermitine genera in South America, and the more specialized genera are associated with derived termite genera of the *Nasutitermes* phyletic line throughout the tropics. This subject is treated in detail in my earlier work (Seevers 1957). The Corotocini, as well as certain other staphylinid tribes, have enjoyed remarkably stable relationships with the Nasutitermitinae. From the present-day host-guest relationships one may deduce a few cases of change in host affinities, but these have had very minor effects on the total pattern of interrelationships. The evolution of the Corotocini, as well as that of the Perinthini and other tribes, evidently took place within the framework of the host phylogenetic pattern; as the termites underwent speciation and generic differentiation, the associated termitophiles evolved new taxa.

The Subtribe Corotocina.—The most highly specialized of the staphylinid termitophiles belong to the Corotocina, a subtribe that includes the new genus *Spirachthodes* and the new species of *Thyreoxenus*. The nine genera of this subtribe, which has a pantropical distribution and a consistent relationship with the *Nasutitermes*-line of Nasutitermitinae, form the following groups: (1) three very closely related genera, *Eburniola* of the Neotropical Region, *Termitoptocinus* of Australia, and *Termitopullus* of the Belgian Congo; (2) *Termitomimus* of the Ethiopian Region; (3) *Corotoca* of northern South America; (4) two genera noted for their unique physothoracic condition (fig. 7), *Thyreoxenus* of the American tropics and Solomon Islands, and *Oideprosoma* of Africa; (5) two genera noteworthy for their distinctive abdominal appendages (figs. 1.3), *Spirachtha* of South America, and *Spirachthodes* of Madagascar. All five of these groups of Corotocina may have stemmed from *Eburniola*-like stock, although this is less evident in the case of *Corotoca*. It may be that all except the *Termitomimus* group originated in the New World. A majority of the Corotocina occur with *Nasutitermes*, some species with the American genus *Constrictotermes*, and a few African species with *Trinervitermes*. It is plausible that the subtribe Corotocina differentiated from generalized corotocine stock in societies of *Nasutitermes*-like hosts.

The discovery of the Madagascan genus *Spirachthodes* adds singificantly to our knowledge of the zoogeography of the Corotocina. Inasmuch as an entire century had passed since the discovery of *Spirachtha* in 1853, it was assumed that the evolution of abdominal appendages was an American evolutionary phenomenon of Tertiary times. It is now clear, of course, that *Spirachtha*-like forms may have reached almost all tropical areas of the world. As termitophiles have not been sought in most parts of the Oriental and Ethiopian Regions, it may be predicted with confidence that additional members of this generic group will be discovered.

The tribe Corotocini, and particularly the subtribe Corotocina, provides excellent examples of the exceptional stability of interspecies systems comprising termite societies and staphylinid inquilines. One example is provided by three very closely allied genera isolated with species of *Nasutitermes* in three continents: *Eburniola*, *Termitoptocinus*, and *Termitopullus* in South America, Australia, and equatorial Africa, respectively. Another illustration is *Thyreoxenus* and *Oideprosoma*, the former in the Americas and Solomon Islands and the latter in west Africa. *Spirachtha* and *Spirachthodes* are a third example of a long established phyletic line. With only these two genera available, we have no clue as to the place of origin of the first genus with abdominal appendages. Subtribal stock from which this phyletic line could have been derived was probably very widespread in the tropical world of the Mesozoic. If there was no truly tropical connection between the Old and New World during the Tertiary, as many students of past climates believe, it is necessary to postulate the existence of the *Spirachtha* phyletic line in the Mesozoic. To have reached Madagascar in the early Tertiary, as seems likely, the specialized ancestor of *Spirachthodes* probably reached the east coast of Africa no later than the Eocene. Emerson (1955) concluded that the Malagasy termite fauna is a segment of the Eocene Ethiopian fauna, and Darlington (1957) drew the same general conclusion about the mammalian fauna. Madagascar, now some 260 miles from the African coast, was doubtless much closer in Cretaceous or early Tertiary times. The water gap was certainly narrow enough to permit termite societies and their associated guests to enter Madagascar. Although poorly investigated, the staphylinid termitophile fauna of Madagascar includes *Millotoca* (closest known relative in Tanganyika), *Termitochara* (closest known relative is probably *Abroteles* of the American tropics), and *Termitana* (closest known relative is *Termitoecia* of Australia).

On the basis of the examples above and many others, I am convinced that most groups of termitophilous Staphylinidae acquired their major adaptive features early in their associations with termite societies and that they have changed very little in long intervening periods. It seems very probable that a number of groups of staphylinids as we now know them were present in the societies of Nasutitermitinae before this group dispersed from South America to the far ends of the earth. Bearing in mind that the Nasutitermitinae and their guests are tropic-limited, it seems essential to account for their dispersal to the Old World in pre-Tertiary times, probably by an Alaskan land connection.

The Subtribe Termitogastrina.—This subtribe

contains one of the more generalized members of the Corotocini (*Termitophya* of the Neotropical Region) as well as some very specialized genera (*Termitoptochus* of the Indo-Australian Region, fig. 8). Numerous genera and species occur in the American tropics with *Nasutitermes*. The Old-World fauna is as yet poorly known, but shows unmistakable evidence of having been derived from the American fauna.

New species of two genera, *Idiogaster* and *Termitoptochus*, are recorded in this paper. The range of *Idiogaster* in the Old World is shown to be extensive, now including India, Eritrea, and Rhodesia. *Idiogaster* is an important genus in

FIGS. 1–6.—*Spirachthodes madecassus*, n. sp. FIG. 1: Lateral view of fully developed imago (sternites 3–8 numbered); FIG. 2: Dorsal view of abdomen (morphologically, the ventral surface), head and thorax not visible from above; FIG. 3: Lateral view of imago with two pairs of appendages; FIG. 4: Ventral view of head; FIG. 5: Maxilla; FIG. 6: Prementum and labial palpi.

linking the palaeotropical fauna of the subtribe to such American genera as *Xenogaster*.

The recording of *Termitoptochus australiensis* adds a new continent to the range of Termitogastrina. *Termitoptochus* belongs to a specialized generic group whose members have large, ovate, membranous abdomens. This group includes *Termitoptochus* (Singapore, the Philippines, Australia), *Millotoca* (Tanganyika, Madagascar), and *Paracorotoca* (South Africa).

The general outline of a theoretical evolutionary history of the Termitogastrina was given in my 1957 paper. The subtribe evidently differentiated in the American tropics in societies of *Nasutitermes*-like hosts. This occurred prior to the dispersal of the Nasutitermitinae to the Old World, probably in the Mesozoic. The American stock of this subtribe became isolated in societies of *Nasutitermes* with which all present-day representatives occur. Subtribal stock that reached the Old World had opportunities to become segregated in societies of genera that differentiated in the palaeotropics: *Bulbitermes*, *Trinervitermes*, *Grallatotermes*, and *Tumulitermes*.

2. *The subfamily Trichopseniinae*

As this subfamily has not been recorded from the Ethiopian Region, its range is greatly extended by the discovery of the new Belgian Congo genus, *Termitona*, whose nearest known relative is *Schizelythron* of Java.

The Trichopseniinae are unusual among termitophilous staphylinid groups in several respects: they are the only termitophilous subfamily of Staphylinidae, they occur in all zoogeographic regions, and they are primarily associated with the family Rhinotermitidae. Morphologically, the Trichopseniinae have a number of specialized features (Seevers, 1941, 1957), and occupy a rather isolated position in the Staphylinidae. Their primary host affinities are with the Rhinotermitidae, a cosmopolitan termite family occupying an intermediate position in termite phylogeny. Members of the subfamily occur with several tropical genera as well as with the north temperate genus *Reticulitermes* in the United States and Japan. The Trichopseniinae generally fall into two categories: physogastric genera such as *Termitona* (fig. 10), and those with a limuloid body form.

Spirachthodes, new genus

Type species: *Spirachthodes madecassus*, new species.

Spirachthodes is remarkably close to the neotropical genus *Spirachtha* Schiödte in basic structure, so that generic diagnosis is dependent largely on differences in the physogastric abdomen. Inasmuch as these differences arise through postimaginal development, it is doubtful if stenogastric individuals have significant diagnostic differences. The newly emerged imago of *Spirachtha* is known to be a winged, stenogastric individual without abdominal appendages (see Emerson 1949, fig. 259); a comparable stage of *Spirachthodes* has not been discovered. The type series of the latter includes an individual that is presumably intermediate between a stenogastric stage and a fully physogastric imago, so there is little doubt that postimaginal development does occur.

The two genera are differentiated on the basis of the following characteristics of fully developed imagos:

1. In *Spirachtha*, the third abdominal segment is conspicuously larger than any of the other segments, which are only moderately swollen and which are nearly uniform in degree of inflation. In *Spirachthodes*, the third segment is large but not appreciably more swollen than the fourth; segments 4–7 decrease gradually in size; and the eighth segment is greatly expanded.

2. In *Spirachthodes*, segments 3–6, and to a lesser degree the eighth, have large areas of secondarily sclerotized integument. The abdomen of *Spirachtha* is largely membranous.

3. The partly sclerotized appendages of *Spirachthodes* are distinctive in form. The membranous appendages of the three species of *Spirachtha* differ somewhat in form so that a generic pattern is difficult to characterize; yet they differ somewhat from those of *Spirachthodes*.

4. The extreme lateral extension of the third and fourth tergites and the development of fourth-segment appendages far up on the sides of the abdomen are distinctive features of *Spirachthodes*.

5. The presence of a second-segment "sternite" characterizes *Spirachthodes*.

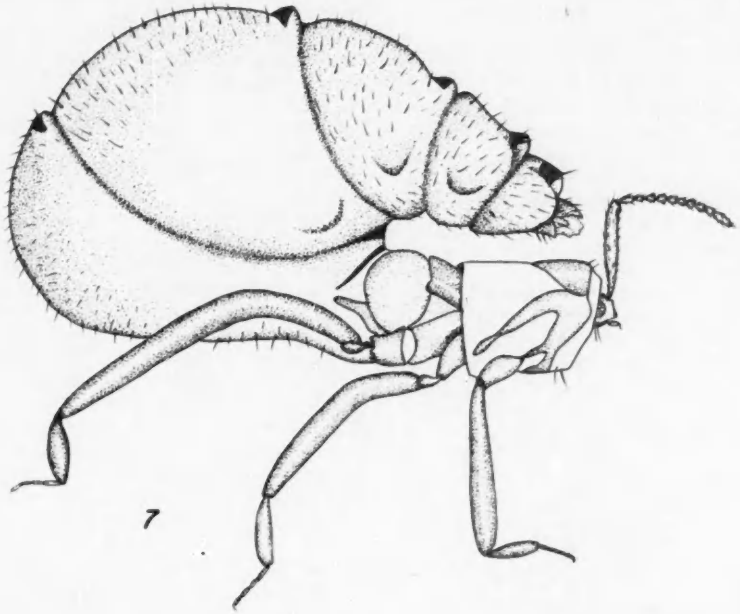
6. *Spirachthodes* has a V-shaped sclerite behind the procoxae (probably formed from the mesothoracic peritremes) not present as such in *Spirachtha*.

7. The fourth segment of the maxillary palpi is present as a pair of long spicules in *Spirachthodes*.

Habitus as in figure 1; head and thorax small and slender; the permanently recurved abdomen extremely inflated and bearing three pairs of semimembranous appendages in fully developed imagos.

Head capsule generalized, circular in outline, subequal in length and breadth; frontoclypeal suture present. Gula (fig. 4) broad at base, its sides converging strongly in front; submentum and mentum fused (a tribal character); prementum moderately long; labial palpi (fig. 6) extremely small, two-segmented, the second segment with a minute spicule; galea (fig. 5) with a row of conspicuous bristles on medial margin, lacinia more slender, arcuate; fourth "segment" of maxillary palpi consisting of two spicules (fig. 5); mandibles with slender, acute tips, the left mandible feebly crenulate. Antennae moderate in length, slender in form, uniform in width, and with most segments slightly elongated.

Prothorax slightly inflated, i.e., with a moderate expansion of membranous integument between prothorax and head and on ventral surface. Pronotum and prosternum generalized. Prothorax with a slender V-shaped sclerite behind procoxae. Mesosternum and metasternum typical of the tribe, i.e., with mesocoxae widely separated and not set in margined acetabula; there are no clearly defined meso- and metasternal processes between them. Hind coxae triangular in form (a tribal



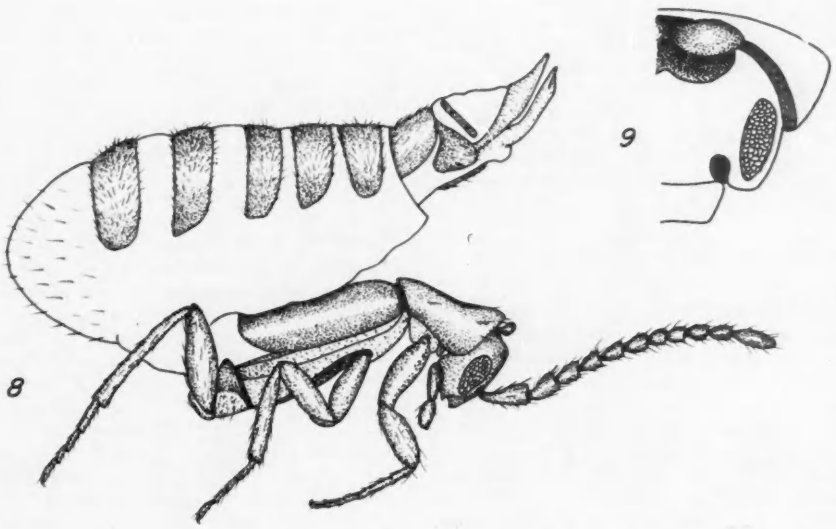


FIG. 7.—*Thyreoxenus mexicanus*, n. sp. FIG. 8.—*Termitoptochus australiensis*, n. sp. FIG. 9.—*T. australiensis*, front view of head and pronotum.

character); the coxae articulating medially with relatively long metasternal processes (a subtribal character). Elytra generalized. Wings absent in fully formed imagos, presumably broken off at base; wings present in the single available imago that has not completed postimaginal changes. Legs without unusual features. Tarsi 4-, 4-, 4-segmented.

Abdomen of imago with three pairs of appendages (figs. 1, 2)

Tergites and sternites of strongly inflated abdomen widely separated. Second segment with a narrow, straplike tergite and an H-shaped "sternite". Tergites of third and fourth segments produced laterally as long, straplike sclerites (in some cases they appear to be fused). Tergites of segments 5–8 small, several not visible in lateral view. Sternites (numbered in fig. 1) small, transverse; third sternite greatly expanded basally through secondary sclerotization to provide strong support for base of abdomen. Sides of abdomen strengthened by extensive sclerotized areas (stippled in fig. 1). Abdomen strongly constricted at level of seventh segment; eighth segment strongly expanded. Three pairs of semimembranous appendages present (figs. 1, 2); these are derived from the fourth, fifth, and sixth segments. Appendages of fourth segment short and claviform; located at the ends of the attenuated fourth tergite. Appendages of fifth and sixth segments bow-shaped, unevenly sclerotized, and moderately setose.

Abdomen of imago with two pairs of appendages (fig. 3)

The following description applies to two specimens in the type series that had not completed postimaginal development: Abdomen very membranous, with little indication of secondary sclerotization; tergites of the second, third, and fourth segments very slender and scarcely produced laterally; appendages of fourth segment absent; appendages of fifth and sixth segments membranous throughout.

Spirachthodes madecassus, new species

Figures 1–6

Head and thoracic sclerites dark reddish-brown, abdominal sclerites varying from light to dark reddish-brown, and unsclerotized areas white to pale straw-colored. Distribution of setae as in figures 1, 2.

Length, 2 mm., with abdomen in recurved position.

Holotype from Ste. Marie de Marovoay, Madagascar; collected September 1, 1911, by W. Kaudern; with the type colony of *Nasutitermes kaudernianus* (Sjöstedt). In collection of Naturhistoriska Riksmuseet, Stockholm, Sweden.

Paratypes.—Eleven specimens, same data as type, in Stockholm Museum and Chicago Natural History Museum.

Remarks.—Almost 50 years have elapsed since this species and its hosts were collected. The first specimen of this notable new genus was found by Dr. Alfred E. Emerson in a vial of host termites sent to him for study by the Stockholm Museum. Later, on a trip to Stockholm, he discovered 11 more specimens with the type series of termites. Inclusion of these beetles with the type termite series was, of course, inadvertent and indicates only that Sjöstedt examined the termite series in a very cursory manner.

Thyreoxenus mexicanus, new species

Figure 7

This species is allied to *brevitibialis* Seevers of eastern Colombia, a guest of *Nasutitermes costalis* (Holmgren). The antennae, with their long scape and short intermediate segments, and the legs, with elongated femora and shortened tibiae, clearly show the two species to be closely allied. In *mexicanus*, these trends have been carried further, with the antennal scape almost as long as segments 2–9 combined (in *brevitibialis*, scape is as long as segments 2 6 combined), and with the much swollen and greatly elongated femora several times longer than the small tibiae (in *brevitibialis*, the hind tibiae are one-half to three-fifths as long as femora).

The only available specimens of *mexicanus* apparently have not undergone complete postimaginal development of abdomen and prothorax. This is judged from the absence of an abdominal "collar" between the sixth and seventh segments and the absence of the secondary sclerotization associated with the sternites in this genus. Inasmuch as these specimens are presumed to be immature in some respects, it is unwise to use the known abdominal characters of *mexicanus* for diagnostic purposes. If this precaution is not kept in mind, it is conceivable that the fully developed imagos may be incorrectly determined as belonging to a different (undescribed) species.

Habitus as in figure 7. Head and pronotum reddish-brown; antennal scape brown, other antennal segments very pale; elytra and abdominal sclerites light-brown; prosternum and legs, except tarsi, rufo-piceous; membranous areas of thorax and abdomen pale straw-colored.

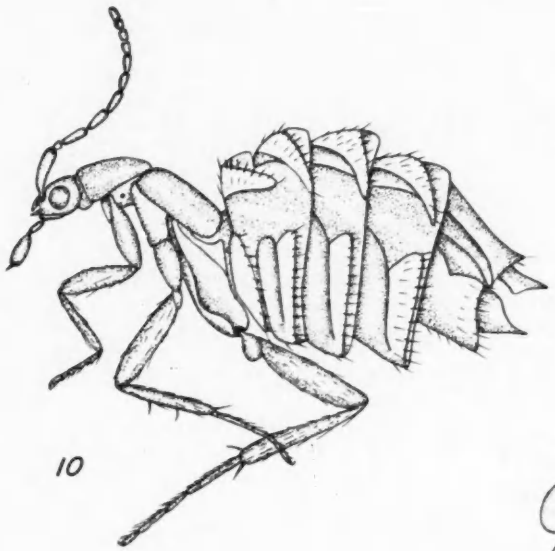
Head very small, generalized in form; almost invisible from above. Antennal scape robust and extremely long, almost equal to segments 2–9 combined; segments 3–9 increasing slightly in length and width; 11 subequal to segments 9 and 10 combined.

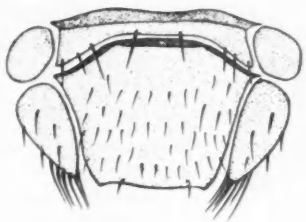
Prothorax (fig. 7) very greatly enlarged and with extensive membranous areas. Prosternum extended up the sides of prothorax to fuse with pronotum; sternonotal suture absent. The trochantins, with which the procoxae articulate, are apparently fused to the prosternum. On the

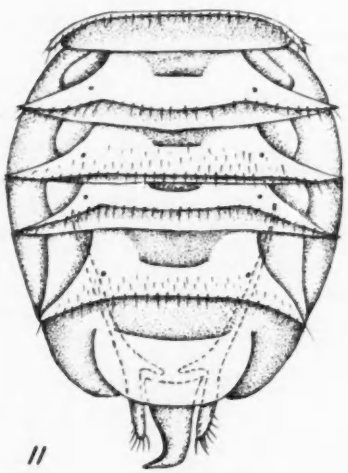
prothoracic sides, the prosternum is produced caudoventrad as a broad process to strengthen the prothorax. The pronotum, prosternum, and trochantins thus form a single sclerite that rings the prothorax. Elytra small. Wings reduced to conspicuous membranous pads behind the elytra (stenogastric individuals are doubtless fully winged).

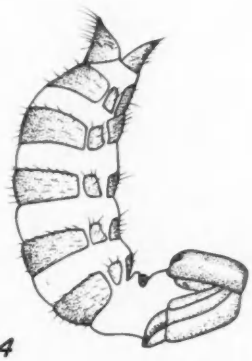
Abdomen of holotype as in figure 7; the segmentation indicated by the sternites on upper surface. Sternite of second segment present. Abdominal sclerites small, generalized in form. Abdomen of holotype without abdominal collar and without secondary sclerotizations usually found in fully physogastric imagos of *Thyreoxenus*.

Legs distinctive; femora remarkably elongated,









FIGS. 10–11.—*Termitona congoensis*, n. sp. Fig. 10: Lateral view; Fig. 11: Dorsal view of abdomen. FIGS. 12–13.—*Idiogaster coatoni*, n. sp. Fig. 12: Gula and submentum; Fig. 13: Sixth and seventh tergites. FIG. 14.—*Protermitobia rhodesiae*, n. sp., abdomen and part of thorax.

bow-shaped; tibiae extremely short; tarsi 4-, 4-, 4-segmented, very slender.

Length, 2–2.5 mm., with abdomen in recurved position.

Holotype from Ciudad del Carmen, Campeche, Mexico; collected January 18, 1939, by A. Dampf (ex collection of Dr. A. Reichensperger); from a nest of termites (doubtless a species of *Nasutitermes*). In collection of Chicago Natural History Museum.

Paratype.—One specimen, same data as type, in collection of Dr. A. Reichensperger, Bad Gödesberg, Germany.

Termitoptochus australiensis, new species

Figures 8–9

This species is distinguished from *T. indicus* Silvestri, 1910 (Singapore), and *T. philippinus* Silvestri, 1921 (Luzon) by the following characteristics: The presence of two membranous lobes between the head and pronotum and deep occipital concavities to receive them; pronotum nearly one-half broader than long and with a diskal impression; head with a vertexal impression.

Habitus as in figure 8. Testaceous, elytra a little darker, membranous integuments of abdomen white. Head with moderately dense punctulation and a moderate number of short erect hairs. Pronotum with medium dense punctulation and short pubescence, and with a few larger setigerous punctures bearing short setae. Sternites with a medium dense punctulation, pale inconspicuous pubescence, and a very few short setae. Membranous integument of third abdominal segment with a conspicuous vestiture of dark setae. Head somewhat deflexed; occiput with two deep concavities to receive membranous lobes arising between the pronotum and head (fig. 9); vertex shallowly impressed. Abdomen strongly physogastric (fig. 8), with large areas of membranous integument; sternites 3 7 straplike, five to six times as broad as long.

Length, 2.1 mm., with abdomen recurved.

Holotype from Williams, Western Australia; collected July 29, 1955, by John H. Calaby from a nest of *Tumulitermes apiocephalus* Silvestri (determined by John Calaby). In collection of Division of Entomology, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia. No paratypes.

Idiogaster Wasmann

Idiogaster Wasmann, 1912, Zeitschr. wiss. Zool., 101, p. 89.
Termitotima Wasmann, 1916, Zool. Jahrb. Syst., 39, p. 188. NEW SYNONYM.

In my 1957 monograph I pointed out that *Idiogaster* Wasmann and *Termitotima* Wasmann are closely allied genera. After a careful comparison of a new species of *Idiogaster* with *Termitotima assmuthi* Wasmann from India, it now seems necessary to combine the two genera.

Idiogaster coatoni, new species

Figures 12, 13

This species differs from *escherichi* Wasmann (Eritrea) in having the pronotum one-half broader than long (three-fifths broader than long in *escherichi*), and in the proportions of some antennal segments: in *coatoni*, segment three is one-half longer than two and a little longer than four; in *escherichi*, segments 2–4 are subequal in length. The seventh tergite of *coatoni* has a relatively dense vestiture of setae; in *escherichi*, only a few irregular rows are present.

The Indian species *assmuthi* (= *Termitotima assmuthi* Wasmann) is closely related to the new species. From *coatoni* it differs in having a nonsetose sixth tergite, in having the pronotum little more than two-fifths broader than long, and in slight antennal differences of doubtful significance (in *assmuthi*, the fourth segment is perhaps a little longer than third).

Coloration light rufo-testaceous.

Head transverse, more than one-third broader than long; vertex with a broad shallow impression extending from base to antennal level. Eyes large. Antennae with segments of the following relative lengths: 34:9:12:11:10:10:10:9:8:8:15. Antennal scape almost as long as segments 2–4 combined; segments 3–5 longer than broad, slightly more slender than the others; segments 5–10 slightly longer than broad or subquadrate; segments 5–11 subequal in width. Submentummentum as in fig. 12; maxillary palpi slender, segments 2 and 3 elongated, somewhat compressed mediolaterally.

Head finely granulose, vertexal impression smooth; pronotum smooth, shining, almost impunctate; elytra sparsely and finely punctate; tergites with a microreticulate sculpture. Tergites of segments 3–6 glabrous except for an apical row of feebly developed setae; seventh tergite (fig. 13) with a moderately dense vestiture of pale setae, many of which are distally curved. Paratergites of seventh segment with a row of about seven closely placed setae; the slender parasternites with several long setae. Sternites 3–5 almost impunctate and with only a few short apical setae. Sternites 6 and 7 with a moderate number of short erect setae; the sixth with an apical row of about 40 long pale recumbent setae, many with curved tips.

Pronotum transverse, one-half broader than long; base arcuate at middle, sinuate laterally; apex slightly arcuate; sides bisinuate, although almost straight in basal one-third. Pronotal surface with a pair of smooth, shallow, foveolate impressions, each with a shallow impression extending caudad; surface, in addition, with a shallow transverse subbasal impression, and an impression near each basal angle so that the angles appear slightly upturned. Elytral inner margins diverging from each other in broad arcs.

Wings reduced, probably broken off near base in physogastric imagos.

The very broad abdomen strongly inflated. Tergites 3, 4, and 5 short, very broad; fifth tergite four times as broad as paratergites. Tergites 6 and 7 (fig. 13) with the typical relationship of all paleotropical species of the subtribe Termitogastrina, but the sixth tergite less modified than in *Termitella* and other genera: sixth tergite slightly bowed, its sides depressed; seventh tergite obtrapezoidal, its posterior angles elevated. Paratergites very broad (but no exception for the subtribe); parasternites slender, those of segments 3–6 incompletely separated from sternites. Apical angles of seventh sternite produced as moderately long blunt processes, each bearing numerous setae.

Length, 4.5 mm., with abdomen extended.

Holotype from Kitwe, Northern Rhodesia; collected by W. G. H. Coaton, January, 1957, with *Trinervitermes* n. sp. (Tm—4035; hosts in Emerson and Coaton collections). In Chicago Natural History Museum.

Paratype.—One specimen, same data as type, in collection of the Division of Entomology, Department of Agriculture, Pretoria, Union of South Africa.

Protermitobia rhodesiae, new species

Figure 14

The genus *Protermitobia* Seevers was proposed in 1957 for two species, *kirbyi* Seevers (Tanganyika), and *comes* Seevers (Sierra Leone). *Protermitobia* belongs to the aleocharine tribe Termitopaediini, an Old World group associated primarily with fungus-growing termites (Macrotermitinae). *Protermitobia* is exceptional in its host relationships, having been found in all cases with *Cubitermes* of the subfamily Termitinae.

P. rhodesiae may be distinguished from its closest ally, *kirbyi* Seevers, by the following characteristics:

In *rhodesiae*, which is a less robust species, the abdomen is 1.35 mm. broad and the pronotum 0.9 mm. broad; the pronotum is broadest subapically, the sides converge evenly to the broadly rounded basal angles; the pronotal surface has a microreticulate sculpture.

In *kirbyi*, the abdomen is 1.8 mm. broad and the pronotum 1.1 mm. broad; the pronotum is broadest one-third the distance from base to apex, and its sides are almost straight; the pronotal surface is very densely, minutely punctulate.

Light-brown, head and thorax a little darker than abdomen (Ndola specimen lighter and more rufous); outer apical angles of elytra, antennae, and parts of legs pale.

Head with numerous fine erect setae; pronotum with 12–14 setae on apical and lateral margins; 2–4 near basal margin, and 8–12 on disk. Elytra very sparsely setose. Tergites sparsely setose. Sternites and parasternites densely setose; eighth sternite with a conspicuous vestiture of moderately long setae along its apical margin.

Head and pronotum finely reticulated, elytra nearly smooth, with traces of reticulation. Head moderately punctate, pronotum sparsely punctate, elytra very sparsely punctate.

Antennae of moderate length, its segments of the following relative lengths: 9:5:5:5:5:5:5:5:5:6:22; basal segment short, very little longer than broad, segments subequal in size, slightly transverse, segment 10 slightly longer; segment 11 much longer than any other segment, somewhat compressed distally.

Pronotum broadest about three-fourths the distance from base to apex; its side margins converging evenly to the rounded basal angles; moderately convex; apex broadly, feebly arcuate; base straight medially, oblique laterally. Elytra elongated; side margins subparallel for a short distance and then diverging moderately to the distinctively modified apical angles: the apical margin is notched so that the apical angles are semidetached. Inner elytral margins strongly arcuate distally. Wings present.

Holotype from Abercorn, Northern Rhodesia; collected in December, 1954, by H. D. Brown; with *Cubitermes* sp. In collection of Chicago Natural History Museum.

Paratypes.—One, same data as type, in Division of Entomology, Department of Agriculture, Pretoria, Union of South Africa. One, Ndola, Northern Rhodesia, collected in January, 1957, by W. G. H. Coaton.

Termitona, new genus

Type species: *Termitona congoensis* new species.

As *Termitona* is the first Ethiopian genus of *Trichopseniinae*, it is necessary to compare it with *Schizelythron* Kemner, 1925, of Java, the closest allied genus in the Oriental Region. The latter has not been available for study so I have had to rely on Kemner's illustrations and description. Although there are several striking differences in the two genera, I judge that they belong to the same phyletic line. Both occur with *Schedorhinotermes*.

Termitona and *Schizelythron* have the same pattern of physogastry, but the tergites and sternites differ appreciably; the tergites of *Termitona* are especially distinctive, being produced laterally as acute processes. The elytra of *Termitona* are generalized while those of *Schizelythron* are remarkably modified: they are split lengthwise for nearly the entire length, and the outer half is extended laterad. The pronotum of *Termitona* is transverse and has no impressions; in *Schizelythron*, the pronotum is elongated and has several impressions. In *Termitona*, the tergite of the terminal male abdominal segment is sickle-shaped; it is probably not this way in *Schizelythron*. The head, mouthparts, and antennae appear to be rather similar in the two genera;

the third segment of the maxillary palpi is unusually large in both cases.

Head two-fifths broader than long, excluding labrum; dorsum unmodified, vertex slightly declivous in front.

First segment of antennae moderately long, somewhat clavate; second segment small; segment three longest of segments 2–11; 3–10 decreasing in length, tenth segment about half as long as third; terminal segment not much longer than tenth.

Pronotum large, transverse; about two-fifths broader than long; anterior margin arcuate; base more nearly straight; broadest in front of middle; dorsum without impressions. Elytra generalized. Metasternum appreciably elongated, extending caudad much beyond apex of elytra; metasternal lobes (a subfamily character) large; metasternum narrowed behind. Hind coxae fused to metasternum (a subfamily character), and not delimited from metasternum. Hind trochanters large, subovate.

Abdomen physogastric (fig. 10); not recurved over foreparts. Tergites and sternites more or less separated by areas of membranous integument, parasternites and paratergites, judging from positions of spiracles not separated from tergites and sternites (a subfamily character). Tergites 3–7 attenuated laterad, produced as acute processes. Tergite of male terminal segment asymetrical, sickle-shaped (fig. 11); lateral plates of terminal segment spatulate, prolonged internally as very long apodemes (a subfamily character). Seventh sternite of female broadly arcuate, and with a shallow median incision that is prolonged on to the surface as a shallow depression; apex of eighth sternite narrow medially and rounded, its sides sloping away strongly; eighth sternite with a narrow, shallow, median impression.

Termitona congoensis, new species

Figures 10, 11

Coloration reddish-brown; membranous areas straw-colored. Head sparsely setose; with one prominent seta medial to each eye. Pronotum microreticulate; disk with a moderate number of setigerous punctures including a medial group that forms a hexagon. Abdominal setae as in figs. 10, 11.

Antennal segments with the following relative lengths: 28: 8: 18: 14: 12: 11: 10: 9: 8: 8: 12; basal segment broad at apex, claviform, its slender proximal portion with a concave undersurface; segment 2 slender; segment 3 twice as long as broad; segments 3–8 longer than broad, 9 and 10 subequal in length and width; segments 3–6 decreasing in length and width; segments 6–10 decreasing in length but increasing in width; segment 11 only a little longer than broad.

Legs moderately long; without unusual features; tarsi 5-, 5-, 5-segmented, elongated, slender, somewhat compressed.

Length, 3 mm.

Holotype from Kisantu, Belgian Congo; collected January 4, 1913, by P. von Wing; from nest of *Schedorhinotermes lamanianus* (Sjöstedt); in Wasmann collection, Natuurhistorisch Museum, Maastricht, The Netherlands.

Paratypes.—Three specimens, same data as type, in the above collection and Chicago Natural History Museum.

Coptotermoecia Oke

Dr. F. J. Gay, Division of Entomology, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia, has kindly called my attention to two incorrect host records in my 1957 monograph. The host of two species, *Coptotermoecia alutacia* Oke, and *Coptotermoecia gayi* Seevers, is *Coptotermes lacteus* (Froggatt), and not *Coptotermes acinaciformis* (Froggatt) as cited.

REFERENCES CITED

Darlington, P. J. 1957. Zoogeography: The Geographical Distribution of Animals. New York: John Wiley and Sons, Inc.

Emerson, A. E. 1949. *In*: W. C. Allee, A. E. Emerson, O. Park, T. Park, and K. P. Schmidt, Principles of Animal Ecology. Philadelphia and London: W. B. Saunders Co.

1952. The biogeography of termites. Bull. Amer. Mus. Nat. Hist. 99: 217–26.

1955. Geographical origins and dispersions of termites. Fieldiana: Zool. 37: 465–521.

Kemner, N. V. A. 1925. Javanische Termitophilen: I, *Schizelythron javanicum* n. g., n. sp., eine neue physogastre Staphylinide von einem neuen, nicht zu den Aleocharíden gehörigen Typus, nebst biologischen Bemerkungen über *Jacobsonella termitobia* Silvestri. Ent. Tidskr. 46: 106–26, 1 pl.

Schiödte, J. M. C. 1853. On some Staphylinidae, found in the nests of termites. Proc. Zool. Soc. London 21: 101–3.

1856. Observations sur des Staphylins vivipares qui habitent chez les termites, à la manière des animaux domestiques. Ann. Sci. Nat. (4), Zool. 5: 169–83, 1 pl.

Seevers, C. H. 1941. Taxonomic investigations of some termitophilous Staphylinidae of the subfamilies Aleocharinae and Trichopseniinae (new subfamily). Ann. Ent. Soc. America 34: 318–49, 3 pls.

1957. A monograph on the termitophilous Staphylinidae (Coleoptera). Fieldiana: Zool. 40: 1–334, 42 figs.

Silvestri, F. 1910. Descrizione di un nuovo genere di Stafilinide termitofilo di Singapore. Boll. Lab. Zool. Portici 5: 37–39, 3 figs.

1921. Descrizione di alcuni Staphylinidae termitofili delle regioni orientale e australiana. Boll. Lab. Zool. Portici 15: 3–23, 14 figs.

Wasmann, E. 1912. Neue Beiträge zur Kenntnis der Termitophilen und Myrmecophilen. Zeitschr. wiss. Zool. 101: 70–115, 3 pls.

1916. Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien, ausgeführt im Auftrage der Kgl. Preuss. Akademie der Wissenschaften zu Berlin von H. v. Buttel-Reepen. V. Termitophile und myrmecophile Coleopteren. Zool. Jahrb. Syst. 39: 169–210, 2 pls.

EFFECT OF AGING AND CONCENTRATION ON THE ATTRACTANCY OF PROTEINACEOUS MATERIALS TO HIPPELATES GNATS[1]

MIR S. MULLA, GEORGE P. GEORGHIOU, AND ROBERT W. DORNER
University of California Citrus Experiment Station, Riverside

ABSTRACT

Aerobic fermentation at 88°±2° F. was found to liberate the attractant principle, at various rates and time-intervals of aging, from various materials exposed and tested in the eye-gnat olfactometer. Fresh preparations of these materials manifested little or no activity. Attractancy of Staley's Corn Protein Bait No. 7 was highest at the end of a 19-day test period; of Staley's Corn Protein Bait No. 2, on the 13th day; of lactalbumin peptone, lactalbumin hydrolysate, and Edamin, on the second day; of autolyzed yeast, brewers yeast, and partially hydrolyzed yeast, on the third, fourth, and seventh day, respectively. Egg albumen was highly attractant around the fourth day of aging, whole egg and egg yolk on the tenth and the sixth day, respectively, though the peak attractancy of the last two to *Milichiella* sp. was indicated around the second day. Homogenates of fresh *Hippelates collusor* and *Musca domestica* were also attractants for eye gnats, but dried *H. collusor* homogenized into water showed no appreciable attractancy. With lactalbumin peptone and whole egg, there was a steady increase in the capture of eye gnats as the concentration of the materials was increased; but with autolyzed yeast this was true only for concentrations up to the 0.5% level.

The use of attractants as baits in combination with an effective insecticide holds great promise for the control of a variety of insect pests. Attractants have also been employed as lures for detecting newly introduced insect pests and measuring population prevalence of insect pests in infested areas. The use of methyl eugenol and protein hydrolysates as lures or baits against the oriental fruit fly, *Dacus dorsalis* Hendel, and the Mediterranean fruit fly, *Ceratitis capitata* (Wied.), is a good example (Steiner 1952a, 1952b). Synthetic materials manifesting attractancy against the gypsy moth, *Porthetria dispar* (L.) and fruit flies have been discussed by Hall et al. (1957). However, no synthetic material is known to attract eye gnats. Protein hydrolysates, ammonium carbonate, and glycine sodium hydroxide lures and baits have been successfully used for the control and measurement of population prevalence of the walnut husk fly (Barnes and Ortega 1958, 1959; Barnes and Osborn 1958).

The use of fermenting proteins as attractants for *Hippelates* eye gnats has been known for almost three decades. The first fermenting type of attractant used for luring *Hippelates* gnats consisted of chopped pork liver in water plus a small amount of urea (Parman 1932; Burgess 1935, 1951). The bait, prior to use in the traps, was fermented for a few days. This same type of bait, aged for 2 weeks at room temperature, was used for studies on eye gnats in Georgia (Dow 1959). Mulla (1958) investigated the effectiveness of several proteinaceous materials used in bait traps in the field as lures for *Hippelates* gnats. When freshly prepared aqueous preparations of these materials were placed in traps it was not until 2 or 3 days later that gnats were attracted. Subsequent observations on the attractancy of these materials indicated an age-attractancy relationship. It was the purpose of this study to examine the effect of aging on the attractiveness of various proteinaceous substances to eye gnats. A limited study of the concentration and response level of eye gnats for some of the materials is also presented.

TESTING PROCEDURE

Aqueous solutions or suspensions of the materials to be tested were prepared. Materials that were not soluble in water were blended with a Waring Blendor. The preparations were subjected to aerobic fermentation under greenhouse lighting conditions at a temperature of 88°±2° F. The concentrations of the preparations are expressed as percent of weight per volume. For aging studies, stock preparations were deep-frozen and replicated aliquots were thawed at intervals and allowed to ferment at constant temperature.

The samples were tested for their attractancy in the Citrus Experiment Station olfactometer (Mulla et al. 1960), except as indicated. Depending on the attractancy of the material and the conditions under which the experiment was conducted, ¼ to ½ ounce of the bait was exposed in each trap. In most cases only gnats that had collected in the vials were counted; however, in a few cases the gnats drowned in the bait dish were also counted. The gnats attracted and captured were mostly females.

The experiments were carried out in the field in an area where populations of *H. collusor* (Tsnd.), *H. hermsi* Sabrosky, *H. robertsoni* Sabrosky, *H. pusio* Loew, and *H. dorsalis* Loew were encountered. The behavior of *H. hermsi* toward many baits is not yet well understood and not enough individuals were captured during this study to make the data applicable to this species. This species, unlike the other

[1]Paper No. 1226, University of California Citrus Experiment Station, Riverside, California. Accepted for publication May 2, 1960. Studies supported by a grant-in-aid from the Coachella Valley Mosquito Abatement District, Riverside County, California. The assistance of Leonard D. Moore of that District is greatly appreciated.

Hippelates observed here, was not readily attracted to fermenting proteins. The populations of *H. robertsoni*, *H. pusio*, and *H. dorsalis* were very low in the study area, but occasionally individuals of these species were caught in the traps. Since these species represented only a small fraction of the total catch, their count was included for convenience with that of *H. collusor*. Therefore, the data in all the experiments bear mostly on the behavior of *H. collusor*. It should be known, however, that the other three species also responded to these baits.

RESULTS AND DISCUSSIONS

Effect of Aging on Attractancy

The effect of aging or duration of decaying process was studied on corn proteins, lactalbumin-like products, yeast products, and egg and fish products.

Corn Proteins.—Two hydrolized corn proteins, Staley's Corn Protein Baits No. 7 and No. 2 (A. E. Staley Mfg. Co., Decatur, Ill.), were evaluated. In experiment A (table 1), 2 percent solutions were aged from 1 to 10 days, and in experiment B (table 1), a new set of solutions was aged up to 19 days.

Table 1.—Attractancy to *Hippelates* gnats of 2 percent solution corn protein bait at various ages of fermentation[a]

Age (days)	Average number of gnats per trap[b]			
	Experiment A		Experiment B	
	Staley No. 7	Staley No. 2	Staley No. 7	Staley No. 2
1	0.0	1	—	—
3	0.0	4	—	—
6	0.0	2	—	—
8	1.5	14	—	—
9	—	—	1.0	14.0
10	13.0	10	—	—
11	—	—	5.7	13.0
13	—	—	2.3	24.3
15	—	—	6.7	15.7
17	—	—	9.0	7.3
19	—	—	22.7	2.7

[a]All ages of each material in each experiment tested on one olfactometer. Therefore, comparison between the two materials in each experiment or between experiments A and B is not valid.

[b]One-half ounce bait used in each trap. Each treatment replicated three times in randomized block design.

Corn Protein Bait No. 7 did not manifest any attractancy until it was aged for 8 days, but Corn Protein Bait No. 2 showed slight attractancy from the outset. Corn Protein Bait No. 7 reached peak attractancy on or beyond the 19th day of aging with lowest attractancy shown on the 9th day of aging period. Corn Protein Bait No. 2, on the other hand, showed increased activity with aging until the highest catch of gnats was obtained at the 13th day. After this period, the attractancy showed a steady decline. At the 19th day of aging the attractancy of this material was the lowest.

Table 2.—Attractancy to *Hippelates* gnats of 2 percent lactalbumin peptone, lactalbumin hydrolysate, and Edamin at various ages of fermentation[a]

Age (days)	Average number of gnats per trap[b]		
	Lactalbumin peptone	Lactalbumin hydrolysate	Edamin
1	52	43	4
2	187	77	76
3	131	32	11
5	51	5	7
7	12	6	7
9	2	6	8
Totals	435	169	113

[a]Each treatment can be compared with others, both horizontally and vertically.

[b]One-half ounce of bait used in each trap. Each treatment replicated three times, one on each of three turntables.

Lactalbumin Products.—Lactalbumin peptone, lactalbumin hydrolysate, and Edamin (Sheffield Chemical Co., Norwich, New York) were evaluated in this group of proteinaceous substances. The age-attractancy relationship of these materials followed more or less the same pattern, and all three materials reached peak attractancy at the second day of fermentation (table 2). After the second day of aging, the attractancy of all three materials dropped gradually. Until the fifth day, however, lactalbumin peptone maintained a fairly high degree of attractancy for the gnats. But at the seventh day of aging, the attractancy of this material was negligible.

It is obvious that lactalbumin peptone manifested greater attractancy at all ages, except the ninth day, than did lactalbumin hydrolysate and Edamin. It is also important to note that lactalbumin peptone and lactalbumin hydrolysate preparations released a greater amount of the attractant material after the first day of fermentation than Edamin did. The overall attractancy of Edamin and lactalbumin hydrolysate seems to be, respectively, approximately one-fourth and one-third that of lactalbumin peptone.

Yeast Products.—Among the yeast products the attractancy patterns of 1 percent preparations made from brewer's yeast and autolyzed yeast (Bioferm Corporation, Wasco, Calif.) followed a similar course (table 3): peak attractancy of the two preparations, determined by the percent collection of gnats (74.5% and 47.8% of the total

capture), occurred after an aging period of 4 and 3 days, respectively. The 1 percent autolyzed yeast produced a second but lower peak of attractancy on the seventh day of aging. Brewer's yeast did not produce this bimodal attractancy pattern, but it did produce one very high peak of attractancy at the fourth day of aging. After the fourth day of aging the attractancy of this material declined sharply.

The attractancy pattern of 4 percent autolyzed yeast differed in two ways from that of the 1 percent preparation. The peak attractancy of the former was delayed until the seventh day, and there was no second peak of attractancy. Relatively high attractancy was manifested by the 4 percent preparation prior to the peak. This suggests two possibilities: (a) a differential in the fermentation rate and process, or (b) a differential in the concentration of attractant principle liberated at the different concentrations of the preparations.

A 10 percent preparation of partially hydrolyzed yeast (Marvin R. Thompson Inc., Stamford, Conn.) was slower in reaching the peak attractancy than the other two materials. The peak attractancy for the partially hydrolyzed yeast was reached 7 days after start of aging. Prior to the seventh day of aging the attractancy was negligible. The attractancy of this material after the seventh day of aging declined gradually with no appreciable second peak of attractancy. The attractancy of the preparation between the peak (seventh day of aging) and the next interval (15th day of aging) was not determined. It is possible that another peak may have occurred during this 8-day interval.

Egg and Fish Products.—Powdered whole egg, egg albumen, egg-yolk powder, and fish meal were evaluated. These, like yeast products, in contrast to lactalbumin peptone, lactalbumin hydrolysate, and Edamin products, are complex proteins and many difficulties were encountered during the aging of these materials.

Table 3.—Attractancy to *Hippelates* gnats of yeast products at various ages of fermentation.[a]

Age (days)	Experiment A Brewers yeast[b] (1%)		Experiment B Autolyzed yeast[c] 1% Concentration		4% Concentration		Experiment C Partially hydrolyzed yeast (10%)[d]	
	Average number gnats/trap	Percent of total	Average number gnats/trap	Percent of total	Average number gnats/trap	Percent of total	Average number gnats/trap	Percent of total
1	0.3	0.5	1.6	2.9	10	8.6	0.2	0.1
2	6.3	10.8						
3			26.6	47.8	11	9.5		
4	43.5	74.5						
5			3.0	5.4	14	12.1	0.2	0.1
6	2.7	4.6						
7			12.0	22.4	47	40.5	130.0	56.2
8	2.0	3.4						
9			3.6	6.4	9	7.7		
10	1.2	2.1						
11			2.6	4.7	3	2.6		
12	1.7	2.9						
13			3.0	5.4	8	6.9		
14	0.7	1.2						
15			1.5	2.7	6	5.2	51.0	22.1
17			1.3	2.3	8	6.9		
19							19.7	8.5
26							27.4	11.9
32							2.6	1.0

[a]Each experiment was run individually; therefore, horizontal comparison among the gnat collections is not possible. One-quarter ounce of bait was used per trap.

[b]Each treatment was replicated six times with two replicates on each of three olfactometers in a randomized block design.

[c]Each treatment was replicated eight times and four times, respectively (for the 1 percent and 4 percent preparations) with two replicates on each of four and two olfactometers.

[d]Eleven replicates on stationary screen frames. Preparations, unlike the others, were aged aerobically in the field.

The attractancy pattern of 2 percent egg albumen showed great activity at the second day of aging and reached the peak near the fourth day of aging (table 4). By the eighth day of fermentation, the attractancy of this preparation was almost completely exhausted. Practically 90 percent of the total catch was accounted for by the combined total catches of the 2- and 4-day-old preparations, leaving the remaining 10 percent collection for

solutions tested 8 or more days after start of the decaying process. The relationship between aging and attractancy of egg albumen is similar to that of lactalbumin peptone (table 2) except that the peak attractancy of the latter preparation was reached slightly earlier.

Table 4.—Attractancy to *Hippelates* gnats of 2 percent egg albumen powder preparations at various ages of fermentation[a]

Age (days)	Number gnats collected/trap			
	Number of replicates[b]	Range	Average	Percent of total catch
2	8	11–47	25.0	15.3
4	8	38–197	121.0	73.8
8	9	1–21	7.0	4.3
12	9	0–10	4.0	2.4
16	9	0–8	3.0	1.8
21	9	0–7	2.3	1.4
25	8	0–3	1.6	1.0

[a]Three separate 100 ml. suspensions of the egg albumen were made for each age. Before use the three portions were combined. One-half ounce of bait was used per trap.

[b]Each preparation was replicated three times on three turntables except for those having eight replicates. In the latter cases, one of the three turntables had only two replicates.

Whole-egg and egg-yolk preparations reached their peak attractancy to eye gnats after 10 and 6 days of aging, respectively (table 5). The attractancy peaks of both these materials were not so sharp as those of lactalbumin peptone (table 2) and egg albumen (table 4). These materials manifested appreciable attractancy to eye gnats at almost all ages tested.

A count of *Milichiella lacteipennis* Loew (determined by Dr. C. W. Sabrosky, U. S. National Museum, Washington, D. C.) attracted to whole egg and egg yolk was also recorded. Here in both cases the peak attractancy was observed on the second day of fermentation (table 5). But large numbers of this species were observed hovering over containers in which whole-egg powder was being mixed with water. It is possible, therefore, that whole-egg or egg-yolk preparations fresher than 2 days might have more attractancy for *Milichiella* than the 2-day-old preparations.

A 10 percent preparation of fish meal manifested peak attractancy to eye gnats after 1 day of aging (table 6). Almost three-fourths of the total gnats captured at all the ages tested were caught by the 1-day-old preparation. The attractancy of fresh preparations as well as of those aged beyond the 1-day period was very low.

The maximum attractancy of proteins on aging as determined by the highest percent fraction of total gnats collected per series is only a relative value with regard to the overall pattern of aging of each material studied. If more and frequent intervals of aging were selected, the peak attractancy values would be smaller. Lower percent fraction values would be obtained by more intervals than by fewer intervals of aging. Nevertheless, the attractancy patterns would be close to those studied here.

Table 5.—Attractancy to *Hippelates* gnats and *Milichiella lacteipennis* of 1 percent preparations of whole-egg powder and egg-yolk powder at various ages of fermentation[a]

Age (days)	Experiment A Whole egg				Experiment B Egg yolk			
	Hippelates gnats		*Milichiella* sp.		*Hippelates* gnats		*Milichiella* sp.	
	Average number/ trap[b]	Percent of total	Average number/ trap[b]	Percent of total	Average number/ trap[b]	Percent of total	Average number/ trap[b]	Percent of total
2	15	4.1	28	43.8	10	3.3	36	28.8
4	32	8.8	9	14.0	35	11.8	13	10.4
6	36	9.9	4	6.3	90	30.0	5	4.0
8	62	17.0	11	17.2	40	13.3	23	18.4
10	102	28.0	7	10.9	—	—	—	—
12	—	—	—	—	48	16.0	19	15.2
14	—	—	—	—	46	15.3	12	9.6
18	50	13.8	5	7.8	—	—	—	—
20	67	18.4	—	—	31	10.3	17	13.6

[a]One-half ounce of bait was used per trap. Experiments on whole-egg powder and egg-yolk powder preparations were performed separately; therefore, it is not possible to compare the magnitude of *Hippelates* and *Milichiella* collections in one experiment with that of the other.

[b]Each treatment was replicated five times on three olfactometers in a randomized block design.

Attractants Emanating from Insects.—During the course of studies on attractants for eye gnats, it has been observed that eye gnats have a tendency to enter more readily into traps where other insects are more active in the vicinity of the traps. It has also been observed that traps baited with materials having little or no attractancy for eye gnats, but having the power to lure large numbers of other species of insects into the bait, trap a good number of eye gnats as well. Short-lived baits such as fish meal and lactalbumin peptone, when allowed to remain in bait traps over a period of several days, will have enhanced attractancy for prolonged periods due to the decaying of insects drowned in the baits. Short-lived baits have been observed to be self-charging when water is available in the bait containers. It is possible that eye gnats are attracted by the movement and chemical odors of other insects as well as of other eye gnats.

Table 6.—Attractancy to *Hippelates* gnats of 10 percent fish meal at various ages of fermentation[a]

Age (days)	Average number gnats		Average total/trap	Percent of total catch
	Bait dish	Vial		
0	0.5	3.4	3.9	6.0
1	11.5	36.6	48.1	74.4
2	0.3	3.1	3.4	5.3
3	0.3	1.6	1.9	2.9
4	0.1	1.0	1.1	1.7
7	0.1	1.5	1.6	2.5
9	0	0.8	0.8	1.2
11[b]	0.1	3.8	3.9	6.0

[a]Each treatment replicated 10 times on stationary screen frames in a randomized block design.
[b]This age material was set first and several gnats were caught before the others were set.

To study the effect of insect odors or decaying insect proteins, homogenates of equal weights of eye gnats and house flies were prepared in water. In one case, the eye gnat sample was dried and then ground in water. Prior to use the samples were kept under refrigeration. The fresh *H. collusor* and *Musca domestica* homogenates proved to be attractant to eye gnats, while the dried *H. collusor* homogenate manifested practically no activity (table 7). The house fly homogenate was less than half as attractant as the fresh *H. collusor* homogenate. The dried eye gnat homogenate showed no attractancy because the decaying process had probably either stopped or slowed down during the drying process. It is likely that the dried gnat homogenate will also manifest attractancy if it is aged properly.

A consideration of the attractancy of some insects to others is very important in formulating a procedure for testing attractant materials. Traps that would require prolonged periods of exposure of candidate attractants for eye gnats, for example, would yield a less critical picture of attractancy than traps that would yield results with shorter exposure periods.

Fermentation Process of Proteins.—The chemistry of fermentation of complex proteins, such as those investigated here, is not clearly understood. The steps involved in the breakdown of the proteins and liberation of attractant principles during the fermentation process are numerous and complex. Undoubtedly many components of the physical and biological environment regulate the speed and direction of the protein-decaying processes.

More than 10 species of bacteria have been isolated from a fermented autolyzed yeast preparation which manifested peak attractancy against eye gnats. Whether one or more of these particular micro-organisms are involved in the effective liberation of attractive odors during the fermentation of proteins is not known. But it is almost certain that during the decaying processes of proteins, micro-organisms of one kind or another play a major role in liberating breakdown products which are attractive to eye gnats. This

Table 7.—The attractancy to *Hippelates* gnats of ground insect homogenates and egg bait at various ages of fermentation[a]

Insects[b] or bait	Concentration	Average number gnats/		Average total
		Bait dish	Vial	
Dried *H. collusor*[c]	0.430 g/50 ml H_2O	0.0	0.37	0.37
Fresh *H. collusor*[d]	1.600 g/50 ml H_2O	5.0	17.50	22.50
Fresh *Musca domestica*[e]	1.600 g/500 ml H_2O	3.5	4.7	8.2
Egg bait	from bait traps	8.7	31.3	40.0

[a]Four replicates randomized on two stationary screen frames. Homogenates were made in the laboratory and refrigerated until used 12 hours after preparation.
[b]Both sexes of both the gnats and flies were used.
[c]Dried for 8 hours in forced-draft oven at 120° F.
[d]Freshly emerged eye gnats, just fed on 5 percent honey solution, were used.
[e]Taken from colony at Citrus Experiment Station.

Table 8.—The attractancy to *Hippelates* gnats of various concentrations of lactalbumin peptone, whole-egg powder, and autolyzed yeast[a]

Concentration (%)[b]	Experiment A[c] Lactalbumin peptone		Experiment B[c] Whole egg		Experiment C[c] Autolyzed yeast	
	Average number/ trap	Percent of total	Average number/ trap	Percent of total	Average number/ trap	Percent of total
0.001	——	——	0	0	1	0.3
0.005	——	——	2	0.3	17	5.0
0.01	1.4	0.2	7	1.1	6	1.8
0.05	17.4	2.1	51	8.5	20	5.9
0.1	22.0	2.6	54	8.9	40	11.8
0.5	125.3	15.1	74	12.2	78	23.1
1.0	161.0	19.3	77	12.7	50	14.8
2.0	214.0	25.8	87	14.3	51	15.9
5.0	289.0	34.9	122	20.1	37	11.0
10.0	——	——	133	21.9	38	11.3

[a]One-fourth ounce of bait was exposed per trap. Each treatment was replicated eight times with two replicates on each one of four olfactometers in a randomized block design.

[b]All dilutions were made from the highest concentration of each material.

[c]Each experiment was run separately and therefore comparison of the gnat collection among the three experiments is not possible.

point was substantiated by testing a 1 percent lactalbumin peptone solution against eye gnats after the solutions had been aged under sterile and nonsterile conditions. The sterile solution attracted no gnats but the nonsterile solution attracted a large number of eye gnats.

In addition to bacteria, a variety of fungi thrived on the preparations during prolonged aging periods. Mold growth posed a serious problem during the aging of whole-egg powder, egg-yolk powder, and partially hydrolyzed yeast. Samples which were discolored or showed the presence of molds proved to be less attractant than other preparations aged for the same length of time but without these developments.

Notwithstanding these limitations, the information pertaining to the age-attractancy relationship of various proteins should prove useful in future work on attractants for eye gnats and related species. At the present time, no synthetic chemicals are known that manifest attractancy against eye gnats. Until such chemicals are found, the possibility of using fermenting proteins in bait sprays for controlling eye gnats holds some promise (Mulla 1959). Also, no proteinaceous substance has been found thus far to manifest attractancy against eye gnats from the outset without undergoing some kind of decaying process. Therefore, information on the aging and attractancy patterns of protein baits is necessary before they can be employed in gnat control.

Effect of Concentration on Attractancy

Three materials, autolyzed yeast, whole-egg powder, and lactalbumin peptone, were tested for their attractancy at various concentrations. Preparations of the highest concentration were aged in ½-pint glass containers for a period corresponding to the approximate peak attractancy period of each material. Serial dilutions were then made from the preparations and were either tested immediately or frozen for future testing.

At the lowest concentration of lactalbumin peptone (0.01 percent), the attractancy was negligible (table 8). At 0.05 percent concentration some attractancy could be noted. A greater jump in activity was observed at the 0.5 percent concentration level. With further increases in concentration there was an increase in response of the eye gnats to the attractant, but this increase was smaller than the one that occurred from the 0.1 percent to the 0.5 percent concentration.

Tests with various concentrations of whole-egg powder also indicated a direct relationship between the concentration and the response of the gnats (table 8). The 0.001 percent preparation manifested no activity under the test conditions. Appreciable activity was not observed until the 0.05 percent concentration level was reached, and from that level upward there was a gradual increase in response.

The autolyzed yeast preparations produced an interesting pattern of attractancy against the gnats. Here relatively good attractancy was manifested at the lower concentrations (0.005 percent to 0.05 percent). The peak attractancy was shown at 0.5 percent concentration (table 8), beyond which there was a decrease in attractancy with an increase in concentration. At the four highest concentrations there seems to be some

repellent action, possibly caused by excessive concentration of attractant.

It should be pointed out that interference among the various concentrations exists when they are tested simultaneously in the same olfactometer. The lower concentrations would have attracted more gnats had the higher, more attractive concentrations been eliminated. This problem of interference has been observed in many olfactometer tests against eye gnats. It may be expected that an attractant will be less efficient in the presence of a more attractive material where there is a strong competition between the two.

The use of fermented proteins as baits in the control of *Hippelates* eye gnats holds promise. The practical concentration of the materials to be used will depend on the type and concentration of the insecticide. Certain insecticides have been found to reduce the attractancy of the bait somewhat at the practical concentrations.

In insecticide-bait combinations, more bait should be used with an insecticide that manifests repellency against eye gnats. It seems that bait concentrations from 0.5 percent to 1 percent would be both economical and feasible to use in bait-spray applications against eye gnats.

REFERENCES CITED

Barnes, M. M., and **J. C. Ortega.** 1958. Glycine-sodium hydroxide solution as an attractant for walnut husk fly. Jour. Econ. Ent. 51(4): 532–4.

1959. Experiments with protein hydrolysate bait sprays for control of the walnut husk fly. Jour. Econ. Ent. 52(2): 279–85.

Barnes, M. M., and **H. T. Osborn.** 1958. Attractants for the walnut husk fly. Jour. Econ. Ent. 51(5): 686–9.

Burgess, R. W. 1935. The eye gant in the Coachella Valley, California. U. S. Dept. Agric., Bur. Ent. and Plant Quar. E–335. 6 pp.

1951. The life history and breeding habits of the eye gnat *Hippelates pusio* Loew in the Coachella Valley, Riverside County, California. Amer. Jour. Hyg. 53(2): 164–77.

Dow, R. P. 1959. A method of testing insect traps and attractants and its application to studies of *Hippelates pusio* and *Culex tarsalis*. Ann. Ent. Soc. Amer. 52(3): 496–503.

Hall, S. A., N. Green, and **M. Beroza.** 1957. Insect repellants and attractants. Jour. Agric. and Food Chem. 5(9): 663–9.

Mulla, M. S. 1958. Recent developments in the biology and control of *Hippelates* eye gnats. California Mosquito Control Assoc. Proc. and Papers 1958: 78–82.

1959. Some important aspects of *Hippelates* gnats, with a brief presentation of current findings. California Mosquito Control Assoc. Proc. and Papers 1959: 48–52.

Mulla, M. S., R. W. Dorner, G. P. Georghiou, and **M. J. Garber.** 1960. Olfactometer and procedure for testing baits and chemical attractants against *Hippelates* eye gnats. Ann. Ent. Soc. Amer. 53(4): 529–37.

Parman, D. C. 1932. A box-type trap to aid in the control of eye gnats and blow flies. U. S. Dept. Agric. Circ. 247. 4 pp.

Steiner, L. F. 1952a. Methyl eugenol as an attractant for oriental fruit fly. Jour. Econ. Ent. 45(2): 241–8.

1952b. Fruit fly control in Hawaii with poison-bait sprays containing protein hydrolysates. Jour. Econ. Ent. 45(5): 838–43.

SEPARATION AND DETERMINATION OF SEMINAL PLASMA AND SPERM AMINO ACIDS OF THE HONEY BEE, APIS MELLIFERA[1]

A. F. NOVAK,[2] M. S. BLUM,[3] S. TABER, III,[4] AND J. A. LIUZZO[3]

ABSTRACT

Quantitative determinations, using microbiological and paper chromatography methods, showed the arginine content of both seminal plasma and spermatozoa of the honey bee to be greater than that of any of the other 14 amino acids found. Difficulties encountered in obtaining large samples prevented making the determinations on a fat-free, ash-free basis.

Information concerning the amino acid content of insect semen is extremely scarce. Therefore, this investigation was undertaken to determine the amino acid content of seminal plasma and sperm of the honey bee.

Protein and amino acid composition of mammalian seminal plasma and spermatozoa has been reported and discussed by Sarkar et al. (1947), Zittle and O'Dell (1941a, 1941b), Porter et al. (1951), Wagner-Jauregg (1941), Jacobson (1950), and Gassner and Hopwood (1952). Free amino acids were shown to be present in fish semen by Steudel and Suzuki (1923). Microbiological and chromatographic methods of analyses were employed.

[1]Accepted for publication April 25, 1960.

[2]Department of Agricultural Chemistry and Biochemistry, Louisana State University, Baton Rouge.

[3]Department of Entomology, Louisana State University.

[4]Agricultural Research Service, U. S. Department of Agriculture.

METHODS AND MATERIALS

The procedure for collecting semen from drone honey bees (*Apis mellifera* L.) has been described by Mackensen and Roberts (1948). Semen for analyses was collected from free-

flying drones, employing extreme caution to exclude any mucus from the semen. By applying pressure to the body, drones were induced to evert and immediately ejaculate.

Immediately after collection, semen from approximately 50 drones was placed in a melting point capillary tube having an inside diameter of 1.8 to 2.0 mm. The semen was centrifuged at approximately 20,000 r.p.m. in a "Misco" electric centrifuge,[5] which caused the sperm cells to settle to the bottom of the tube leaving the sperm-free, clear seminal plasma occupying the upper part of the tube. The proportion of seminal plasma to sperm varies from 1:1 to 1:2, depending upon the season. Semen centrifuged at 20,000 r.p.m. for 20 minutes has been used successfully to inseminate queens to fertilize eggs. Therefore, it is unlikely that mechanical damage to sperm cells resulted in contaminating the plasma with proteins extracted from the sperm cells as suggested by Mann (1954).

Hydrolysis was accomplished by autoclaving 100 mg. samples of seminal plasma and sperm with 10 ml. of 6 N HCl in small Pyrex tubes for 4 hours at 121° C. Excess HCl was removed by evaporation to dryness on a steam bath, and the amino acid hydrochlorides were desiccated over NaOH for 2 days. This acid hydrolysate was used for the determination of all amino acids except tryptophane, which was released by alkaline hydrolysis. For tryptophane analysis 100 mg. samples were placed in small Pyrex tubes and hydrolyzed in 10 ml. of 14% $Ba(OH)_2$ by autoclaving 18 hours at 121° C. Barium was removed with a slight excess of 1 N H_2SO_4 and the $BaSO_4$ precipitate was thoroughly washed with hot water containing a trace of acetic acid. The filtrate was concentrated to a small volume in vacuo and evaporated to dryness over $CaCl_2$ in a desiccator.

Aliquots for assay were prepared from these hydrolysates of seminal plasma and sperm, and results were reported as the amounts of bound amino acids, that is, requiring some form of protein hydrolysis prior to determination of the total quantity of each amino acid present. Seminal plasma was analyzed also for its free amino acid content, and the results were reported as such. No preliminary hydrolysis of this sample was necessary.

Microbiological and paper chromatography methods were employed for the amino acid determinations. Commercial media obtained from Difco Laboratories, Inc. (Difco Manual 1953) were used where applicable because these products are highly standardized and the results obtained can be duplicated reasonably.

Dehydrated Bacto Tryptophane Assay Medium, employing a culture of *Lactobacillus arabinosus* 17–5 ATCC 8014, was used for the microbiological determination of tryptophane.

Dehydrated Bacto Assay Media, designed for each amino acid to be measured and utilizing a culture of *Leuconostoc mesenteroides* P–60 ATCC 8042 as the assay organism, were used for the microbiological assays of arginine, cystine, leucine, isoleucine, lysine, methionine, phenylalanine, and tyrosine.

For comparative purposes and where microbiological procedures were not available, paper chromatography methods of analyses were selected for identification of the amino acids. The methods of McFarren (1951) and McFarren and Mills (1952) were used for the separation of each amino acid from others in the mixture by one-dimensional chromatography, employing several solvents buffered at a selected pH.

Table 1.—Amino acid content of seminal plasma and sperm of the honey bee (milligrams per gram).

	Seminal plasma		Sperm[a]
	Free	Bound	Bound
Tyrosine	0.37	0.46	8.20
Methionine	0.28	0.32	4.70
Leucine	0.46	0.57	12.50
Cystine	0.38	0.44	7.80
Isoleucine	0.42	0.51	5.90
Tryptophane	0.31	0.48	4.10
Lysine	0.73	0.92	12.60
Phenylalanine	0.44	0.60	9.30
Arginine	1.20	1.37	39.20
Glutamic acid	0.87	1.03	10.40
Glycine	0.19	0.38	6.40
Alanine	0.20	0.44	7.10
Aspartic acid	0.23	0.37	6.70
Serine	0.32	0.41	5.80
Threonine	0.11	0.26	3.79

[a]Includes free amino acids also.

Paper chromatograms were buffered by immersing the paper into a buffer of desired pH and molarity, and air-drying, and by equilibrating the solvent with the same buffer instead of water. All solutions were adjusted to a pH between 6.0 and 7.2 prior to spotting to prevent drifting of some amino acids in the mixtures and to obtain reproducible values for those difficult to isolate such as arginine and lysine. Whatman No. 1 paper was used, and 5 µl. to 20 µl. of the solutions to be analyzed were applied. Phenol was selected as the solvent for separating aspartic acid, glutamic acid, serine, glycine, threonine, and alanine. Lutidine was employed as the solvent for arginine and lysine. After drying, the chromatograms were dipped in water-saturated butanol containing 0.4% ninhydrin, and the color developed by drying the chromatogram at 60° C. for 15 minutes. The amino acids were separated into individual and well-defined spots which made the identification of each amino acid in an unknown mixture

[5]Microchemical Specialties Company, Berkeley, California.

possible. This method eliminates the need of resorting to special reagents to confirm the identity of one or more of the amino acids.

The amino acids were then determined quantitatively by maximum density measurements with a photovolt densitometer fitted with a No. 570 filter.

Results are listed in table 1. Each value is the average of duplicate samples on two assays. Minimum variations were obtained and were considered to be within limits of experimental error for each type of determination.

RESULTS AND DISCUSSION

Both free and bound amino acids are found in seminal plasma of the honey bee. Difficulties encountered in obtaining large samples prevented these determinations from being made on a fat-free, ash-free basis. However, these results show the presence of many amino acids in seminal plasma and sperm of the honey bee, and the relative amounts of each. A high arginine content in the sperm suggests comparison with the protein composition of bull semen (Sarkar et al. 1947, Porter et al. 1951). The conspicuously high content of arginine was in the sperm, although the proportion of arginine exceeded that of any other amino acid in the seminal plasma. Lysine and glutamic acid were also high in comparison to the other amino acids present in both sperm and seminal plasma. The leucine content was as high as lysine and glutamic acid in sperm but much lower than these two compounds in seminal plasma.

REFERENCES CITED

Difco Laboratories. 1953. Difco Manual. 8th edition. Detroit, Michigan. (pp. 212–36).

Gassner, F. W., and **M. L. Hopwood.** 1952. Seminal amino acid and carbohydrate pattern of bulls with normal and abnormal testes function. Proc. Soc. Exptl. Biol. and Med. 81: 37–43.

Jacobson, L. 1950. Free amino acids in human semen. Acta Physiol. Scand. 20: 88–90.

Mackensen, O., and **W. C. Roberts.** 1948. A manual for the artificial insemination of queen bees. U.S.D.A., Bur. Ent. and Plant Quar. ET–250.

Mann, T. 1954. The Biochemistry of Semen. New York: John Wiley & Sons, Inc. 194 pp.

McFarren, E. F. 1951. Buffered filter paper chromatography of the amino acids. Analyt. Chem. 23: 168–75.

McFarren, E. F. and **J. A. Mills.** 1952. Quantitative determination of amino acids on filter paper chromatograms by direct photometry. Analyt. Chem. 24: 650–3.

Porter, J. C., S. Shankman, and **R. M. Melampy.** 1951. Chemical composition of bovine semen. Proc. Soc. Exptl. Biol. and Med. 77: 53–56.

Sarkar, B. C. R., R. W. Luecke, and **C. W. Duncan.** 1947. The amino acid composition of bovine semen. Jour. Biol. Chem. 171: 463–5.

Steudel, H., and **K. Suzuki.** 1923. Zur Histochemie der Spermatogenese. Zeitschr. Physiol. Chem. 127: 1–13.

Wagner-Jauregg, T. 1941. Uber das Vorkommen des Heptakosans in menschlichen Sperma. Zeitschr. Physiol. Chem. 269: 56–58.

Zittle, C. A., and **R. A. O'Dell.** 1941a. Chemical studies of bull spermatozoa. Lipid, sulfur, cystine, nitrogen, phosphorus, and nucleic acid content of whole spermatozoa and of the parts obtained by physical means. Jour. Biol. Chem. 140: 899–907.

1941b. Chemical studies of bull spermatozoa. The methionine content of whole spermatozoa and of the parts obtained by physical means. Jour. Biol. Chem. 141: 239–43.

SEASONAL HISTORY AND REARING OF SCAPHYTOPIUS ACUTUS (SAY) (HOMOPTERA: CICADELLIDAE)[1]

D. H. PALMITER, W. J. COXETER AND J. A. ADAMS[2]

New York State Agricultural Experiment Station, Geneva and Poughkeepsie, N. Y.

ABSTRACT

Seasonal fluctuations in populations of *Scaphytopius acutus* (Say), a vector of X-disease virus, were followed for a 5-year period in a peach orchard by means of sticky-board traps. Supplemental records were obtained from traps exposed near other cultivated and wild *Prunus* species. The first adults were usually found early in June. Two distinct broods were recorded each year, with adult peaks occurring about July 1 and October 1. The greatest numbers of adults were taken in traps hung in, or near, peach, apple, plum, and chokecherry (*P. virginiana* L.). A laboratory method was developed for hatching overwintered eggs found in apple and stonefruit leaves. High relative humidity and temperatures near 70° F. provided optimum conditions for hatching. Apple and chokecherry seedlings were found to be suitable host plants for the rearing of nymphs and adults. There was evidence of an overwintering diapause: eggs laid by the second-brood adults did not hatch in the fall.

Scaphytopius acutus (Say)[3] was first reported as a vector of Western X-disease virus by Anthon and Wolfe (1951). Hildebrand (1953) reported the occurrence of *S. acutus* on the hosts of X-disease in New York and suggested a vector relationship. Gilmer and McEwen (1958) re-

[1]Approved by the Director of the New York State Agricultural Experiment Station for publication as Journal Paper No. 1216 March 31, 1960. Accepted for publication April 13, 1960.

[2]Respectively, Professor of Plant Pathology, former Experimentalist in Plant Pathology and Associate Professor of Entomology, New York State Agricultural Experiment Station.

[3]Specimens collected and used for reference in this investigation were identified by David A. Young, Entomology Research Division U. S. D. A., Washington, D.C.

ported transmissions of X-disease in New York by this leafhopper. Wolfe (1955) listed alfalfa as the most common host of *S. acutus* in Washington but indicated that both nymphs and adults were found in abundance on a species of sticky laurel (*Ceanothus*) at higher elevations in August. Besides peach and sweet cherry trees, wild rose, willow, sumac, Oregon grape and certain species of *Spirea*, *Cirsium* and *Populus* were listed as host plants. He indicated that *S. acutus* overwintered in the egg stage and had two broods during the season. Little further information on the life history of this leafhopper and its host relationship with stone-fruit trees susceptible to X-disease is available.

This paper is a summary of findings regarding the life history of *S. acutus* obtained in the course of investigations on the control of X-disease in the Hudson River Valley in New York. In experiments with insecticide applications as a means of preventing the spread of X-disease in peach orchards, trends in leafhopper populations in sprayed and unsprayed plots were followed by means of sticky-board traps (Palmiter and Adams 1957). In order to have sufficient leafhoppers available for transmission tests, it was necessary to know their life history and to work out a method of rearing them in the laboratory. The information obtained is summarized for others interested in leafhoppers as virus disease vectors.

FIELD OBSERVATIONS

Nymphs.—Nymphs of *S. acutus* were seldom caught on trap-boards in peach trees. To determine their presence and location, early-season observations and sweepings of ground-cover were performed. In 1959, second-instar nymphs were observed on ground-cover by May 25, and the first adults were caught on trap-boards exposed between June 1 and 12 near chokecherry (*Prunus virginiana* L.). Nymphs were observed feeding on alfalfa (*Medicago*), trefoil (*Lotus*), red clover (*Trifolium*), sweetclover (*Melilotus*), sheep sorrel (*Rumex acetosella* L.), and chickweed (*Stellaria*). Nymphs seemed to prefer the lower sides of the leaves for feeding; adults were frequently observed on the upper sides.

Trapping of adults.—Sticky-board trap collections and sweepings in the area of Poughkeepsie were started on a regular schedule in 1955. In 1955 and 1956 the traps were placed in peach trees only; but in 1957, 1958, and 1959 they were also placed in cherry, plum, pear, and apple orchards. Other traps were located in thickets of chokecherry, wild black cherry (*P. serotina* Ehrh.), and wild plum (*P. americana* Marsh.). The chrome-yellow boards were 5 by 10 inches, coated with a proprietary adhesive ("Tanglefoot") and were hung on branches or rod supports.

The first adults appeared around the end of the first week of June in each year except 1958, when they were present a month earlier. The peak of first-brood adult captures on trap-boards occurred in the last week of June or in the first two weeks of July (fig. 1). The peak of second-brood captures occurred between mid-September and mid-October. Adults were found in peach orchards in rather high numbers until the end of October. By the first week of November, the peach trees had usually dropped their leaves.

The low catch during the first-brood period in 1957 might be attributed to one or both of two unusual conditions in that season. One was the mass spraying of the area with DDT solutions performed by airplane, around June 6, by the United States Department of Agriculture, for the control of gypsy moth (*Porthetria dispar* (L.)). The other was the occurrence of five frost, or near-frost, periods during May when the leafhopper was in the nymphal stages.

The 1955 records of *S. acutus* in this orchard were similar to those for 1959 except that the second-brood peak occurred in September instead of October. The first- and second-brood peaks in 1956 corresponded with those of 1958 but the numbers of leafhoppers collected were much smaller in 1956.

The numbers of *S. acutus* caught per 10 traps exposed during the 1958 season in different locations averaged 246 for peach orchards, 225 for apple, 180 for cultivated plum, 175 for chokecherry and wild black cherry, 138 for pear, 74 for sweet cherry (*P. avium* L.), 65 for wild plum and 33 for red sour cherry (*P. cerasus* L.). In 1959 only four locations were used and collections were highest on chokecherry (182), equal on peach and wild plum (75 each) and lowest on wild black cherry (27).

The male leafhoppers evidently matured first; trap-board catches in June and early July usually contained twice as many males as females. In general, the males outnumbered the females during the first brood. During the second brood the males were the more numerous from mid-July to mid-September but the total second-brood numbers were evenly divided between the sexes.

Besides *S. acutus* several other leafhoppers were found on trap-boards in peach orchards between June 1 and November 7, 1959. Listed in the order of their abundance they were *Graphocephala coccinea* (Forster), *Colladonus clitellarius* (Say), *Macropsis trimaculata* (Fitch), *Paraphelpsius irroratus* (Say), and *Scaphytopius frontalis* (Van D.).

LABORATORY METHODS AND OBSERVATIONS

Rearing methods.—Fallen leaves were used as a source of eggs. Leaves of peach, chokecherry, wild black cherry, and apple were collected from the field in November 1957 and stored in an open shed until needed. The first leaves were brought into the laboratory in January. They were spread out in 1½ by 4-foot metal trays with

sand in the bottoms and were kept moist by means of an "atomizer" hand sprayer used once or twice daily. The temperature varied from 70° to 75° F. and the relative humidity of the rearing room was kept between 50 and 65 percent. From the eggs contained in these leaves, rearing to the adult stage was accomplished. When eggs in known numbers were wanted, the leaves were examined under a dissecting microscope and those containing eggs were saved. In this way a given number of eggs could be selected and placed under conditions for hatching in small chambers or vials. Hatched nymphs could then be placed on caged plants.

Sweetclover seedlings in small pots were placed in the trays of leaves to provide a source of food for the hatched nymphs. Fluorescent lights were operated over the trays to provide light for the plants. *S. acutus* nymphs and adults developed satisfactorily on sweetclover but the plants were difficult to handle when more than 8 inches high as they became tangled and hard to separate. Apple seedlings were later substituted for sweetclover because the nymphs and adults could be seen and handled more easily on the larger leaves. In 1959 chokecherry seedlings were also used since they served as host plants for *Colladonus clitellarius* as well as for *S. acutus*. Periwinkle (*Vinca*) was tried as a host plant but caged nymphs and adults failed to survive on it for more than a few days.

Duration of stages.—In the rearings in 1958, with a temperature range of 70° to 75° F., *S. acutus* eggs hatched in 11 to 14 days. Adults were available 20 to 25 days after hatching and they remained alive for 20 to 30 days. In 1959, at slightly lower temperatures (65° to 70° F.) eggs in overwintered apple leaves hatched over a period of 13 days, with the first nymph recorded on the 18th day and the last on the 30th day. The following nymphal periods were recorded for a nymph feeding on red clover in the rearing room in 1958: 1st molt on the 2nd day, 2nd molt on the 9th day, 3rd molt on the 11th day, 4th molt on the 15th day and the 5th molt on the 23rd day.

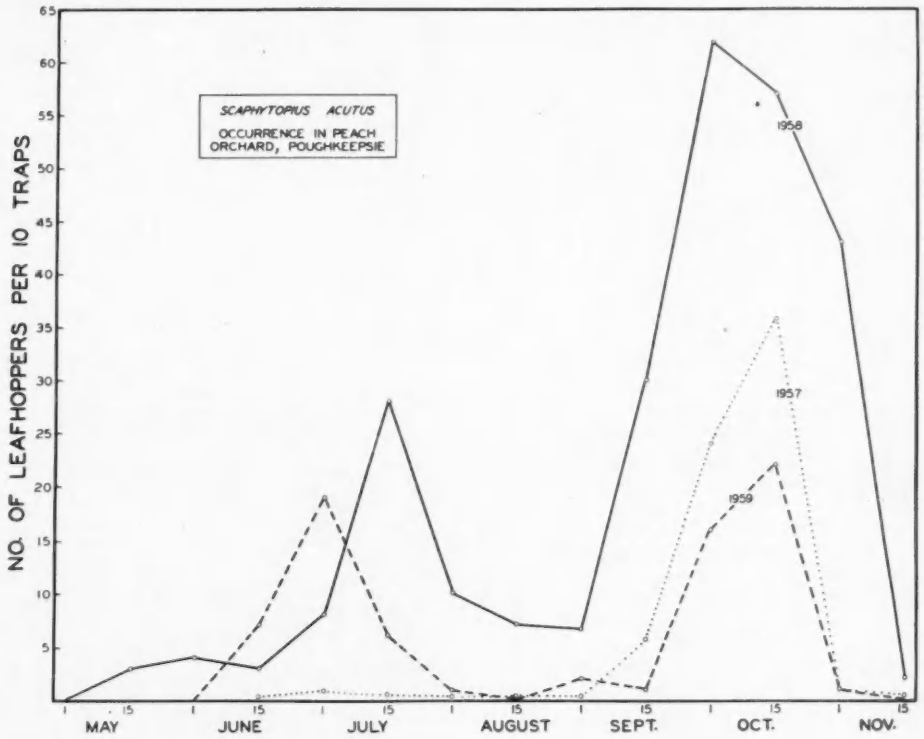


FIG. 1.—Numbers of adult *Scaphytopius acutus* taken on sticky-board traps in a peach orchard at Poughkeepsie, N. Y. in 1957, 1958 and 1959. Leafhopper captives were counted weekly but the data are condensed to show the accumulated captures for semimonthly periods.

The numbers of adult leafhoppers obtained from fallen leaves varied considerably according to the number of eggs present, and the temperature and humidity at which they were held. In 1958, from 16 to 50 adults were obtained from various bushels of peach and chokecherry leaves. In 1959, 42 nymphs hatched from a bushel of apple leaves kept in trays.

Effect of temperature and humidity on egg hatch.—Experiments using controlled temperature and humidity were set up in 1959 to determine the optimum conditions for the hatching of overwintered eggs. Portions of apple leaves containing eggs were cut out and 25 or more eggs were used for each test. There was some hatching at temperatures between 65° and 96° F. but none at 58° or at 98° F. At 69° to 72° F. hatches of 100 percent were obtained when the relative humidity was kept near 100 percent. Of two groups of eggs held at 96° only a small proportion hatched; the resulting nymphs were more than normally yellow-colored and their fat bodies, visible ventrally, appeared to have an orange color rather than the normal yellow. None survived for 24 hours.

Overwintered eggs in apple leaf sections were placed in vials with cotton plugs and kept at relative humidities of 20, 35, 50, 80, 95, and 100 percent. The relative humidities were regulated by various concentrations of sulfuric acid in water within closed jars. This test was conducted at a controlled temperature of 69° F. At each relative humidity 25 eggs were used. There was no hatch below 80 percent relative humidity. At 80, 85, and 100 percent relative humidity 24, 48, and 88 percent hatches were obtained, respectively. In another test at the same temperature the leaf sections containing the eggs were moistened periodically with a few drops of water in addition to being kept at 100 percent relative humidity. In this case all of the eggs hatched during an 11-day period. In the rearing room in 1958, the daily wetting of the leaves in the open trays must have been an important factor in the hatching of eggs, since the relative humidity of the air in the room ranged from 50 to 65 percent.

Location of eggs.—Out of 100 eggs examined on Fall Pippen apple leaves, 85 percent were inserted into the epidermis on the lower sides of the leaves, 9 percent were in the upper epidermis and 6 percent were in matted leaf hairs. The eggs were laid singly and usually only one or two were found to a leaf.

Evidence of diapause.—Eggs from leafhoppers of the first brood, laid on apple seedlings in the rearing room, hatched in 15 to 20 days from the time the adults were caged. Eggs laid by adults collected in the field in October and caged on apple or periwinkle plants failed to hatch when kept under conditions favorable for hatch of eggs from the first brood. This fact may be evidence of a diapause similar to that reported by George and Davidson (1959) as occurring in *Colladonus clitellarius*. Exposure to low temperatures and a longer rest period are probably prerequisites for the hatching of second-brood eggs. Eggs exposed to winter temperatures and brought into the rearing room hatched as early as January.

REFERENCES CITED

Anthon, E. W., and **H. R. Wolfe.** 1951. Additional insect vectors of Western X-disease. Plant Dis. Reporter 35(8): 345–6.

Gilmer, R. M., and **F. L. McEwen.** 1958. Insect transmissions of X-disease virus. Phytopathology 48(5): 262.

George, J. A., and **T. R. Davidson.** 1959. Notes on life-history and rearing of *Colladonus clitellarius* (Say). Canadian Ent. 91(6): 376–9.

Hildebrand, E. M. 1953. Yellow-red or X-disease of peach. Cornell Univ. Agric. Expt. Sta. Mem. 323. 54 pp.

Palmiter, D. H., and **J. A. Adams.** 1957. Seasonal occurrence of leafhopper vectors of X-disease virus in sprayed and unsprayed peach blocks. Phytopathology 47(9): 531.

Wolfe, H. R. 1955. Leafhoppers of the State of Washington. Washington Agric. Expt. Sta. Circ. 277. 35 pp.

SCIENTIFIC NOTES

Laminating Moth Wings and Larvae[1]

MARLIN S. CONRAD[2]

In most institutions there is a limitation on space. A process has been devised whereby reference material for certain groups of insects can be assembled in a compact unit (fig. 1). Fessenden (1949) described the preservation of plant material by lamination, and the preservation of both plants and insects in plastic blocks. His methods were complex and expensive.

Lamination of moth wings and larval integuments has definite limitations, and is not designed to replace mounted or preserved specimens used for comparison studies in detailed taxonomy. These laminated specimens are, however, designed for use by untrained light-trap operators, for sight identification, display work, education, and other purposes where chaetotaxy and body parts are not essential for identification.

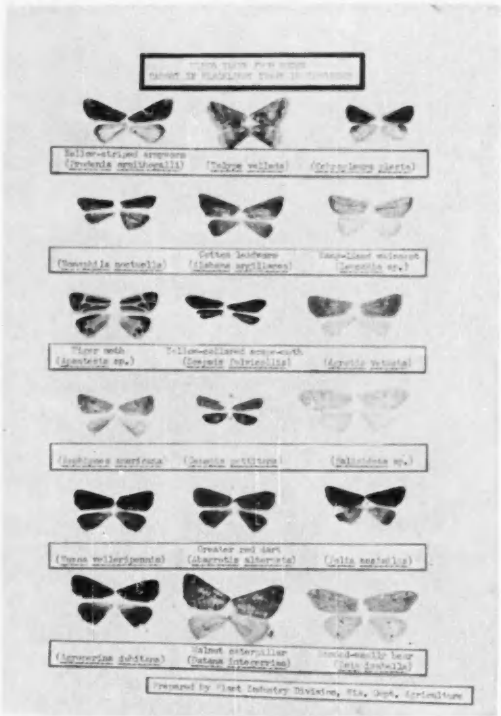


FIG. 1.—Laminated moth wings.

METHODS AND PROCEDURES

Sheets of transparent cellulose nitrate, 8×11×0.015 inches, were used because of their availability. Wings of previously identified moths were removed from the bodies, and a drop of n-butyl acetate was applied to each. Each wing was arranged and placed on a sheet of the "plastic," with the upper surface of the wing in contact with the sheet. Slight pressure was applied with forceps, and the wings were allowed to dry. Typewritten labels were then applied below the sets of wings. These carried both the scientific name and the common name (if approved) on one side, and the family name as well as a number for indexing purposes on the other. Since the typing was found to blur when it came in contact with the n-butyl acetate, a few drops of clear nail polish or of plastic cement were used to secure the labels. After the wing groupings and the labels had been applied, a thin stream of n-butyl acetate was laid along the border of the "plastic" sheet, and a second sheet was applied. The sheets were then welded together by applying pressure along the borders. It was found advisable to scatter a few drops of clear nail polish between the wing groups before fusing the plastic sheets.

Cellulose nitrate may not still be available. Comparable results were obtained by substituting cellulose acetate and by using nail-polish remover (amyl acetate) as a bonding agent. The procedure was the same as with the nitrate sheets.

Favorable results were obtained also in mounting larvae by this method. Larvae, previously preserved in alcohol, were bisected along the middorsal and midventral lines and the body contents were removed. After the integument had dried for a few minutes, a layer of clear nail polish was applied to the inner surface. The larvae were then placed on labeled 2×5-inch cards, two per card, pressed firmly on them with forceps, and allowed to dry. The cards were then bonded to a sheet of "plastic," with a space of ½ inch between rows. A second sheet of plastic, with portions cut out to allow space for the larvae, was then bonded to the bottom sheet with n-butyl acetate, both at the edges and in the spaces between the cards, and finally a third sheet of the "plastic" was cemented over the top with n-butyl acetate.

Larval specimens mounted by this method showed no signs of shrinkage or discoloration more than 3 months later. However, laminated mounts of both moth wings and larvae had a tendency to warp if improperly stored.

The advantages of this method lie in simplicity of construction, inexpensiveness, versatility, and compactness.

REFERENCE CITED

Fessenden, G. R. 1949. Preservation of agricultural specimens in plastic. U. S. Dept. Agric. Misc. Publ. 679.

[1]Approved for publication by the Wisconsin Department of Agriculture. Accepted for publication March 24, 1960.

[2]Entomologist, Wisconsin Department of Agriculture, Madison, Wisconsin.

Empty Cocoons of the Introduced Pine Sawfly, *Diprion similis*, as Habitat Niches for Arthropods[1]

HARRY C. COPPEL[2]

Mature larvae of the introduced pine sawfly, *Diprion similis* (Htg.) usually spin their cocoons on the needles, twigs, and trunks of white pine trees. This is particularly so with the first generation and partially so with the second generation in Wisconsin. The cocoons are attached firmly to the substrate and may remain for 5 years or more after the adults have emerged. During emergence, the adult sawflies cut a sizable cap off the end of the cocoon and thus leave a readymade cell for

[1]Approved for publication by the Director of the Wisconsin Agricultural Experiment Station. This work was supported by a grant from the Wisconsin Conservation Department. Accepted for publication April 11, 1960.

[2]Department of Entomology, University of Wisconsin, Madison 6, Wisconsin.

use by many arthropods. In both 1958 and 1959, at least 10 percent of the empty cocoons from both current and previous years were used as shelter or nesting niches by arthropods sometime throughout the summer.

Collections of cocoons populated by arthropods were made throughout June, July, and August in Polk County, Wisconsin, in 1959. The cocoons were placed singly in glass vials which were then plugged with cotton. Spiders and other immature arthropods were reared whenever possible to provide mature individuals for determination. A total of 195 cocoon inhabitants was handled in this manner.

The following checklist includes all arthropods encountered in 1959. Numbers in parentheses refer to the number of individuals of each species.

Arachnida
- Acarina
  - Erythraeidae
    - *Erythraeus* sp. (1)
  - Leptidae
    - *Leptus* sp. (2)
  - Oribatulidae
    - *Zygoribatula* sp (1)
  - Phytoseiidae
    - *Typhlodromus* sp. (1)
- Araneida
  - Argiopidae
    - *Araneus* sp. (5)
  - Clubionidae
    - *Clubiona pygmaea* Banks (2)
    - *Clubiona* sp. (2)
  - Dictynidae
    - *Dictyna annulipes* Blackwall? (17)
    - *Dictyna sublata* (Hentz)? (9)
    - *Dictyna* sp. (6)
  - Micryphantidae
    - *Ceraticelus atriceps* O. P. Cambridge (1)
    - *Ceraticelus agathus* Chamberlin (1)
  - Salticidae
    - *Admestina tibialis* (C. L. Koch) (60)
    - *Icius* sp. (3)
    - *Metaphidippus* sp. (2)
    - *Paraphidippus marginatus* (Walck.) (1)
    - *Paraphidippus pineus* Kaston (11)
    - *Paraphidippus* sp. (6)
  - Thomisidae (4)
    - *Philodromus rufus* Walckenaer (1)

Insecta
- Coleoptera (1)
  - Coccinellidae
    - *Hulsantina picta* (Rond.) (1)
  - Chrysomelidae
    - *Glyptoscelis* sp. (14)
- Corrodentia
  - Psocidae
    - *Peripsocus madidus* (Hg.) (3)
    - *Peripsocus* sp. (1)
  - Diptera
  - Acroceridae
    - *Acrocera* n. sp. (1)
- Hemiptera
  - Miridae (1)
- Homoptera
  - Aphidae
    - *Cinara* sp. (1)
  - Cicadellidae
    - *Oncopsis variabilis* (Fitch) (1)
    - *Typhlocyba* sp. (1)
- Hymenoptera
  - Braconidae
    - *Aphidius* sp. perhaps *obscuripes* (Ash.) (1)
    - *Meteorus* sp.
  - Formicidae
    - *Leptothorax ambiguus* Emery (2)
  - Tenthredinidae (2)
  - Vespidae
    - *Ancistrocerus tigris tigris* (Sauss.) (13)
- Lepidoptera (2)
- Neuroptera
  - Chrysopidae
    - *Chrysopa* sp. plorabunda group (12)
  - Hemerobiidae
    - *Hemerobius* sp. (1)

OBSERVATIONS AND DISCUSSION

The empty cocoon of the introduced pine sawfly, fixed to its substrate, provides a static habitat niche for many arthropod species. There is no faunal succession correlated with the aging of the cocoon; thus arthropods found in the cocoons late in the season are rarely, if ever, related to or dependent upon those present early in the season. This habitat type differs considerably from those recorded by Graves (1960), who studied the changing fauna of woody shelf fungi throughout their period of decomposition, and by Winston (1956), who carried on the same type of studies with acorns. Apparently the empty cocoon niche has not been investigated previously. The arthropods are discussed in the same order as they appear in the listing.

ACARINA.—Only four species of mites were obtained from the cocoons and these were determined to genus only. Erythraeid, Leptid and Phytoseiid mites are considered predaceous or parasitic on arthropods. *Leptus* sp. is the common red immature mite observed frequently on first-generation larvae of the introduced pine sawfly. The Oribatid mites are known as the beetlemites and feed largely on fungi and other organic matter. The cocoons were probably being used by the mites for shelter.

ARANEIDA.—Six families of spiders were represented in the cocoon collections. They were the most common arthropods and contributed two-thirds of the total arthropod population. *Araneus* sp. (Argiopidae, orb weavers) was not common and was obtained only in the immature stages. The sawfiy cocoons were being used as shelters. *Clubiona pygmaea* Banks (Clubionidae, sack spiders) was uncommon, as only 2 adult females and 2 immatures were collected. These spiders are apparently common on tree and shrub vegetation where they often roll leaves. The sawfly cocoons were being used as nesting sites and for shelter. The Dictynidae or cribellate spiders were fairly well represented with *Dictyna annulipes* Blackwall? being almost twice as common as *Dictyna sublata* (Hentz)? As the sawfly cocoons were being used for nesting sites, females were most common. Determinations in this group are usually made on the basis of male characteristics; thus the question of specificity arises. Only single female specimens of *Ceraticelus atriceps* O. P. Cambridge and *Ceraticelus agathus* Chamberlin (Micryphantidae, dwarf spiders) were obtained. The latter apparently is a first record for Wisconsin. The cocoons were being used as nesting sites. The Salticidae or jumping spiders were the most numerous and were represented by four genera. *Admestina tibialis* (C. L. Koch) was the most common species encountered, contributing almost 46 percent to the total spider population. *Icius* sp. was uncommon, as were *Metaphidippus* sp. and *Paraphidippus marginatus* (Walck.). *Paraphidippus pineus* Kaston was second in importance among the Salticidae. All the Salticidae, with the possible exception of some of the immatures, were females and were utilizing the empty cocoons as nesting sites. *P. marginatus* is known to be predaceous on adults of the introduced pine sawfly. *P. pineus* is apparently a new record for Wisconsin. *Philodromus rufus* Walckenaer (Thomisidae, crab spiders) was uncommon but the female obtained apparently was using the cocoon as a nesting site.

INSECTA.—With the exception of approximately three species, all the insects were represented by single specimens. The Coccinellid, *Hulsantina picta* (Rond.) was

obtained in late August from a cocoon in which it was probably preparing to overwinter. The Chrysomelid, *Glyptoscelis* sp. was one of the common species utilizing empty cocoons. Adult beetles feed on needles of white pine and when the mated females are ready to deposit eggs they drop them into the cocoons in large numbers. The opening is then covered with a disc of wood-chip material for protection. Nothing further is known of the life history of *Glyptoscelis*. Some of the cocoons containing eggs and larvae of *Glyptoscelis* were parasitized, the parasites being entirely hymenopterous species as follows: *Eupelmus* sp., *Habrocytus thyridopterigis* How., *Dahlbominus fuscipennis* (Zett.) and *Eupelmella dryorhizoxeni* (Ashm.). *D. fuscipennis* is an European parasite of pine sawflies, including the introduced pine sawfly. The bark louse *Peripsocus madidus* (Hg.) (Corrodentia: Psocidae) was utilizing cocoons for shelter. The only dipteron obtained was a new species of *Acrocera*. This genus is normally parasitic on spiders and the specimen probably developed within the cocoon. A mirid adult (Hemiptera) was obtained and may be considered an adventive or was using the cocoon for shelter. This is also probably true of the pine-feeding *Cinara* sp. (Homoptera: Aphidae) and the tree- and shrub-inhabiting *Oncopsis variabilis* (Fitch) and *Typhlocyba* sp. (Homoptera: Cicadellidae). Two parasitic species, *Aphidius* sp. perhaps *obscuripes* (Ash.) and *Meteorus* sp. (Hymenoptera: Braconidae), were obtained from cocoons but their hosts are unknown. It is probable that their development was completed in the cocoon shelter. The ant *Leptothorax ambiguus* Emery was obtained from ground-level cocoons. This species is known to nest in small cavities, acorns etc. and may have been using the cocoons as a nesting site.

Only two undetermined hymenopterous larvae (Tenthredinidae) were collected in the cocoons. These were utilizing the cocoons for shelter but after 2 months had not spun their own cocoons and were preserved. Though not recorded as occupying empty cocoons in the list, mature larvae of the introduced pine sawfly, *Diprion similis* (Htg.) often spin their cocoons in this location. The solitary wasp, *Ancistrocerus tigris tigris* (Sauss.) (Hymenoptera: Vespidae) was one of the more common of the insect inhabitants of empty sawfly cocoons. Some of the wasps were parasitized. The European parasite *Monodontomerus dentipes* (Dalm.), an important parasite of *D. similis* in Wisconsin, was obtained as well as three undetermined ichneumonids. Two undetermined lepidopterous larvae were collected and were probably utilizing the cocoons for shelter. The Neuroptera were represented in the cocoons by both Chrysopidae and Hemerobiidae, the former in the larger numbers. Larvae, pupae, and adults of *Chrysopa* sp. *plorabunda* group were all obtained, the immature larvae utilizing the cocoons as shelter, the mature larvae as a protected place in which to spin their cocoons, and the adults as a shelter during the initial stages of emergence. Only one cocoon of *Hemerobius* sp. was observed in an empty cocoon and this later produced an adult.

SUMMARY

Naturally occurring empty cocoons of the introduced pine sawfly provided nesting and shelter habitats for many arthropod species including the Araneida (2.6%), Acarina (67.2%), and Insecta (30.2%). Of those utilizing the cocoons, only the spider *P. marginatus* and the mite *Leptus* sp. were observed feeding on adults and larvae, respectively, of the introduced pine sawfly. The occurrence of *D. fuscipennis* as a parasite of the beetle *Glyptoscelis* sp. and *M. dentipes* as a parasite of *A. t. tigris*, a solitary wasp, is of interest particularly as they are normally sawfly parasites of European origin.

ACKNOWLEDGMENTS

The author is grateful to the following specialists for identifying the many species collected: P. D. Ashlock, E. W. Baker, B. D. Burks, J. P. Kramer, K. V. Krombein, E. L. Mockford, C. F. W. Muesebeck, S. Parfin, L. M. Russell, C. W. Sabrosky, M. R. Smith, and G. B. Vogt of the U.S.D.A., Agricultural Research Service or U. S. National Museum staffs (insects and mites); A. L. Turnbull, Entomology Research Institute for Biological Control, Belleville, Canada, (spiders); and I. M. Newell, U. of California (Leptus sp.).

REFERENCES CITED

Graves, R. C. 1960. Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. Ann. Ent. Soc. America 53: 61–78.

Winston, P. W. 1956. The acorn microsere, with special reference to arthropods. Ecology 37: 120–32.

Lack of Elevated Respiration in Injured Pupae of the Southern Armyworm, *Prodenia eridania* (Lepidoptera)[1]

CHRISTYNA E. MECCA[2]

National Institute of Arthritis and Metabolic Diseases, National Institutes of Health, U. S. Department of Health, Education, and Welfare, Public Health Service, Bethesda, Maryland

Sussman (1952) and Schneiderman and Williams (1953) showed that very minor damage to the cuticle of the diapausing *Cecropia* pupa induces a significant and long-lasting elevation of oxygen uptake rate. Schneiderman (1957) noted that this elevated injury respiration is not seen in *Galleria* pupae (nondiapausing), but no actual data were presented. Since experiments were planned in this laboratory involving the injection into *Prodenia eridania* (Cram.) pupae of materials that might in themselves have effects on the respiratory rate, it was necessary to test the effects of sham injection on this nondiapausing species. At the same time, opportunity was taken to follow the oxygen uptake rate of normal pupae throughout development, which has not previously been done in this species.

METHODS

The pupae were collected from kale-fed cultures within 3 hours after pupation and stored at 25° C, in humidified petri dishes. Under such conditions adult emergence usually occurs on the 10th to 12th day after pupation. Oxygen uptake was measured by Warburg manometry at 25° C., using one pupa per 15-ml. flask. Pupae were weighed before each period of respirometry and respiratory rates were computed in relation to live weight at the time of measurement. The average initial live weight per pupa was 220.52 mg., with a range from 171.2 mg. to 258.2 mg. Four control pupae were studied throughout development, their respiration being measured daily for 2 to 6 hours. Twelve experimental pupae were used, two being punctured on the day of pupation at 5±3 hours of age, and two on each alternate day thereafter. The respiratory rates of several of the experimental pupae were measured on one or more days prior to puncture (i.e., they served as additional controls) and in all cases respiration was measured for 2 hours before and after injury on the day of injury, and for at least 2 hours daily thereafter until eclosion.

Standard cuticle puncture was produced on immobile pupae anesthetized with carbon dioxide, by penetrating

[1]Accepted for publication July 28, 1960. Partial cost of publication of this paper was met by the National Institute of Arthritis and Metabolic Diseases, Department of Health, Education and Welfare, Bethesda, Md.

[2]Present address: National Institute of Dental Research, National Institutes of Health, U. S. Department of Health, Education, and Welfare, Public Health Service, Bethesda, Maryland.

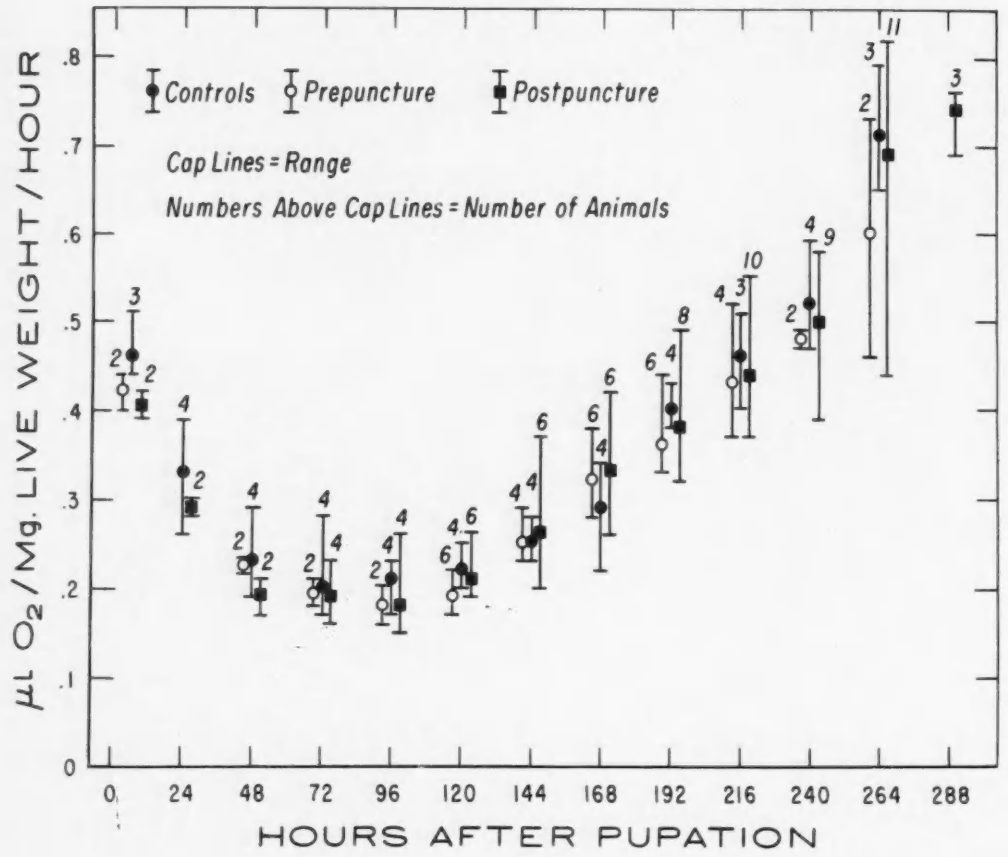


FIG. 1.—Rates of oxygen uptake of *Prodenia* pupae.

the intersegmental membrane between the third and fourth abdominal tergites, about 1 mm. to the right of the middorsal line, using a #30 hypodermic needle. The needle was inserted in an anteroventral direction with the beveled surface down (i.e., with the bevel roughly parallel to the dorsal surface of the pupa) and only just breached the cuticle without penetrating the viscera. A minute drop of blood usually welled out of the wound when the needle was withdrawn, but no significant bleeding occurred.

RESULTS AND DISCUSSION

During the entire pupal period[3] the average weight loss was 26.3 mg. in the controls and 22.4 mg. in the experimentals, or respectively, 12.3% and 9.8% of the initial average weights.

The results of the respiration measurements on *P. eridania* throughout its pupal period until time of emergence are summarized in fig. 1. This figure shows that *Prodenia* pupal respiration follows the usual U-shaped course for nondiapausing insects, falling to a minimum of about 43% of the initial value approximately one-third of the way through pupal life, then rising to about 65% above the initial value close to the time of eclosion. It will be noted also that the variation in respiratory rates at a given age was quite small. As compared with *Galleria*, a similarly nondiapausing form of comparable weight (Bell 1940), *Prodenia* respiration is proportionately the same; that is, for *Galleria*, the low period is about 43% below the initial value and at the time of eclosion the respiration increases to about 70% above the initial value.

As can be seen from fig. 1, the oxygen uptake rate of animals after cuticle puncture was not measurably different from the oxygen uptake rate of uninjured controls at any age. All injured animals emerged normally. According to Schneiderman (1957), *the simple insertion and withdrawal of a fine needle in the diapausing pupa evokes a doubling or tripling of the oxygen consumption within 24 hours.* Schneiderman believed that in the diapausing pupa a trigger mechanism increases oxygen consumption upon the slightest injury. There appears to be no similar triggering apparatus in *Prodenia* pupae when injured with a fine needle, although it is possible that a larger injury would elevate respiration. The present finding therefore agrees with Schneiderman's unpublished finding on *Galleria*. From the practical standpoint the results indicate that materials can be injected into *Prodenia* pupae at any age with the assurance that an elevated respiratory rate is not due to injury.

[3] *Pupal period* is used in the sense of true pupal life plus pharate adult development (Hinton 1948).

REFERENCES CITED

Bell, J. 1940. The heat production and oxygen consumption of pupae of *Galleria mellonella* at different constant temperatures. Physiol. Zool. 13: 73–81.

Hinton, H. E. 1948. On the origin and function of the pupal stage. Trans. Roy. Ent. Soc. London 99: 395–409.

Schneiderman, H. A. 1957. Onset and termination of insect diapause. *In*: T. H. Bullock, ed., Physiological Triggers (pp. 46–59). American Physiological Society.

Schneiderman, H. A., and **C. M. Williams.** 1953. Metabolic effects of localized injury to the integument of the *Cecropia* silkworm. Anat. Rec. 117: 640–1.

Sussman, A. S. 1952. Tyrosine and the respiration of pupae of *Platysamia cecropia* L. Biol. Bull. 102: 39–47.

Territorialism and Residentiality in a Dragonfly, *Orthetrum albistylum speciosum* Uhler (Odonata: Anisoptera)[1]

YOSIAKI ITO[2]

Although territorial behavior of male dragonflies has been reported by many authors, how long the dragonflies which have acquired their territories remain in their respective established places is not exactly known. From his extensive observations on many dragonfly species, Moore (1952) concluded that marked dragonflies sometimes visited the same place on different days, but found this to be exceptional rather than the rule.

Orthetrum albistylum speciosum is a sexually dimorphic dragonfly with clear wings, of moderate body size. The abdomen of the female is black, with yellow stripes and spots. The teneral male closely resembles the female in color, but the abdomen of the mature male is white dorsally. As a rare case, a female with white abdomen (i.e., a "male-type" female) has been reported.

A study of this dragonfly was made at the garden of the National Institute of Agricultural Sciences, Tokyo, from September 7 to 21, 1959. Most of the territory holders within the area where the observations were made were painted with cellulose paint, using a small squirt-gun. In general, observations were made twice each day, at 8:30 to 9 a.m. and at 12:30 to 1 p.m.

In the daytime each mature male of this species restricted his activities to a watered place, where an oviposition site was present, and defended the place against other males of the same species. During the nights, and on rainy days, all individuals left these places. Figure 1 shows the distribution of individual territories in the area surveyed, and table 1 shows the individual territory owners recorded at the respective locations.

This table shows clearly that males with established territories tended to return to their original sites on the next morning, or on the return of suitable weather. For example, male 01 appeared at a paddy field (No. III) for 4 successive days, and male 08 appeared at another paddy field (No. VII) for 6 days intermittently. Thus

[1]Submitted through T. C. Schneirla and sponsored by M. J. Westfall, Jr. Accepted for publication March 7, 1960.

[2]Department of Biology, Tokyo Metropolitan University, Tokyo, Japan.

Table 1.—Changes of territory holders within the area surveyed. Localities I–VII are those shown in fig. 1. The respective numbers in the table are those of marked male individuals; if enclosed in parentheses, this territory holder was expelled by another male during the observation. An unmarked male is indicated by ♂, and other symbols used are: —, no observation made; =, no territory owner present; +, ownership undecided, with violent combat in progress; *, drought conditions in this locality.

Date, Sept. 1959	Location								Weather
	I	II	a	III	b	V	VI	VII	
7, p.m.	01	—	—	—	—	—	—	—	Clear
8, p.m.	01	—	—	—	—	—	—	—	Clear
9, a.m.	03	01		05		04	—	—	Slightly cloudy
9, p.m.	03	01		05		04	—	—	Clear
10, a.m.	=	01		05		04	07	—	Cloudy
10, p.m.	=	=		05		04	07	—	Cloudy
11, a.m.	—	—		05		=	07	08	Slightly cloudy
11, p.m.	10	01		05		09	(04)	08	Clear
12, a.m.	♂	=		05		09	07	08	Slightly cloudy
12, p.m.	12	=		(05)		09	11	08	Slightly cloudy
13, p.m.	12	=		♂		=	13	08	Cloudy
14, a.m.	=	=		=		=	=	=	Rain
15, a.m.	=	=		10?		=	=	=	Slightly rainy
15, p.m.	17	=		♂		♂	18	(08)	Clear
16, a.m.	24	=		23		=	=	08	Slightly cloudy
16, p.m.	26 +♂	—		—		—	08 +♂	—	Clear
17, a.m.	=	=		=		=	=	=	Rain
17, p.m.	(30)	=		23[a]		♂	—	27	Cloudy
18, a.m.	♂	=		+		♂	28	—	Clear
18, p.m.	33	34	23		32	—	♂	16?	Clear
19, a.m.	33	=	23		32	34	=	—	Clear
19, p.m.	33	(36)	32		35	34	=	—	Clear
20, noon	♂	=	33		40	=	=	23	Clear
21, a.m.	42	=	41		40	23?	*	—	Clear
21, p.m.	42	40	=		44	23	43	39	Clear
22, a.m.	=	=	=		44	=	=	=	Cloudy

[a]Intense fighting; no established territory holder.

residentiality, like that reported for *Rana clamitans* by Martof (1953), is well evolved in this dragonfly species. Changes in ownership of a territory seemed to occur when a prior owner was exhausted, or when he was defeated by a more vigorous male after violent combat. Immature males were easily driven away by older, white-colored ones. Exhausted males tended to appear on smaller, and possibly less suitable, sites, as with males 01, 23, and 40.

Whenever a male intruder appeared on the territory of a certain male, the owner dove at the intruder and pursued him 5 to 10 meters away from his territory. On the other hand, when a female appeared the owner seized her, then copulated, and after this the owner released the female and guarded her while she oviposited. In some cases, however, females began oviposition and were guarded by the respective owners without copulation occurring between them. A territory owner might copulate with many females that visited his territory at different times, and a female might also copulate with many males, but no female copulated with a male which did not defend a territory. These matters are, in

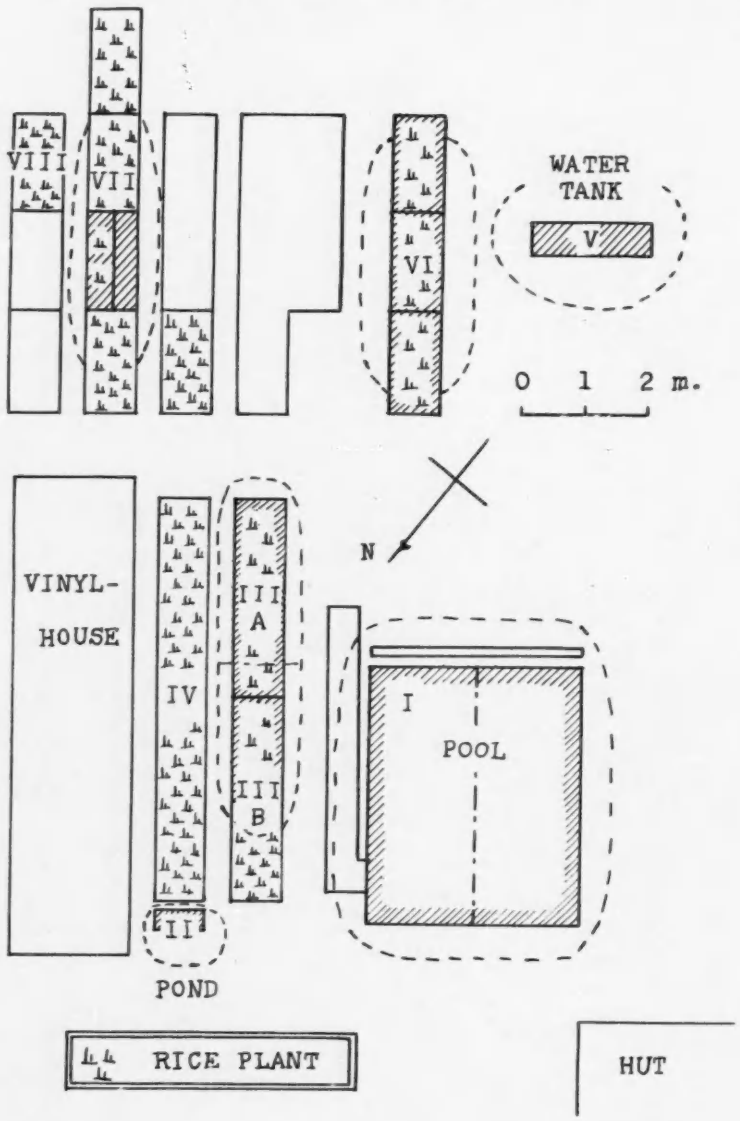


FIG. 1.—Distribution of territories held by *Orthetrum albistylum speciosum* males in the area surveyed. Hatching indicates exposed water surfaces.

general, similar to the observations of Jacobs (1955), except that he could not distinguish courtship behavior from the threat display between males (such as "dual flight" seen in *Plathemis*).

A male-type female appeared during the period of observation, and was seized in normal fashion by male 08 and by another, unmarked male, without any aggressive behavior on the part of the males. Thus discrimination of sex by males may be due not only to differences in color patterns, but also to possible, delicate behavioral differences.

REFERENCES CITED

Jacobs, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology 36: 566–86, 7 figs.

Martof, B. 1953. Home range and movements of the green frog, *Rana clamitans*. Ecology 34: 529–43, 7 figs.

Moore, N. W. 1952. On the so-called "territories" of dragonflies (Odonata-Anisoptera). Behaviour [Leiden] 4: 85–100, 1 fig.

OBITUARIES

Harry Gardner Barber
1871-1960

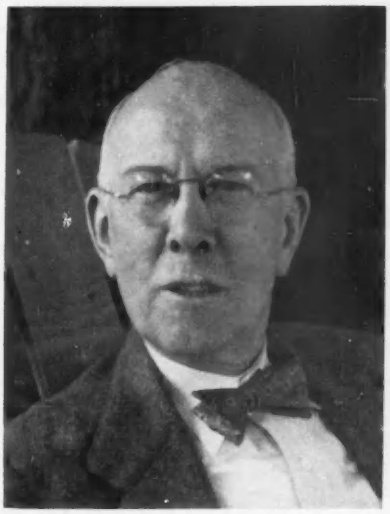
Mr. Harry Gardner Barber, a charter member of the old Entomological Society of America died January 27, 1960 at the age of 88. He was born in Hiram, Ohio on April 20, 1871. In 1881 his parents moved to Lincoln, Nebraska, where his father assumed a position as Professor of Latin and Greek in the newly organized University of Nebraska. In 1893 Mr. Barber graduated from the University of Nebraska and for the next 2 years served as an assistant to Professor Lawrence Bruner in the Department of Entomology. In 1895 he received his Masters Degree. During 1896 he taught science in the Nebraska City High School where he met and subsequently married Blanche E. Davis. In 1897 he undertook graduate work at Bussey Institute, Harvard, and was awarded a Masters Degree by that institution in 1898. From this date until 1930 he taught biology at the DeWitt Clinton High School in New York City. After he retired from teaching he was immediately employed by the U. S. Department of Agriculture as a taxonomist in charge of the true bugs, suborder Heteroptera, a position he held until 1942. At this time he left Washington, D. C. and returned to his earlier home at Roselle, New Jersey, where he lived until Mrs. Barber died in 1949. The last 10 years of his life were spent in Washington where he resumed his work on Heteroptera as a Collaborator of the Entomology Research Division, U. S. Department of Agriculture.

During Mr. Barber's long career, he published only one paper directly concerned with applied entomology. This was entitled "Experiments With Infectious Diseases for Combating the Chinch-bug." It appeared in 1894 in co-authorship with Professor Lawrence Bruner and was the first of the 110 papers he was ultimately to write. It is interesting to note that he had originally intended to specialize on butterflies but the destruction of his entire collection by fire discouraged him from continuing and perhaps because of his work with the chinch bug he turned his attention to the Hemiptera. His only other venture outside the field of Hemiptera was a paper listing the butterflies of Nebraska that was also published in 1894.

During the years that he taught biology at DeWitt Clinton High School, his long summer vacations were spent collecting Hemiptera in many different parts of the United States. Mrs. Barber usually accompanied him on these trips and encouraged him to develop his avocation. It was in this way that he built his fine collection of Hemiptera. He also acquired an outstanding library and through his work and correspondence became recognized as the leading world authority on the family Lygaeidae.

In view of his intense interest in entomology it is scarcely surprising that he also participated in the formation of the Entomological Society of America. This Society was organized in 1906 at a meeting held in the American Museum of Natural History, and Mr. Barber became one of the 364 charter members. Only 20 of these survive him. Subsequently in 1930 he was elected a Fellow and in 1957 became an Emeritus Member of the Entomological Society of America.

Although Harry Barber was a first-class teacher, the daily routine of teaching biology to large classes of boys, city-born and bred, and most of whom had little



HARRY GARDNER BARBER

real interest in the subject, must at times have been trying. Undoubtedly he found relaxation and intellectual stimulation from his week-end and long summer collecting trips as well as from his correspondence with hemipterists in all parts of the world. In 1914 he collected extensively in Puerto Rico for the American Museum of Natural History and thus established an interest that culminated in 1939 in one of his most important and useful publications, that treating the Hemiptera-Heteroptera of Puerto Rico and the Virgin Islands (exclusive of the Miridae and Corixidae). He subsequently extended his interests to Cuba and in cooperation

with Dr. S. C. Bruner eventually published on most of the Heteroptera fauna of that Island.

The last decade of Mr. Barber's life was in many ways the most productive of his career. He donated his fine Hemiptera collection and many of his books to the Museum. As a Collaborator of the Entomology Research Division, he was given desk space and facilities to carry on his work and until well into the last year of his life was to be found daily at his desk almost as though he were a regular employee on the staff. During this last period in Washington he published 17 papers, mostly of revisional or faunal nature, the most important of these being the Lygaeidae section of the Insects of Micronesia, which appeared in 1958. He properly regarded this as his second-best piece of work, surpassed only by the comprehensive paper on the Heteroptera of Puerto Rico. His last paper, completed in the latter part of 1959 with the help of Peter D. Ashlock appeared in the June 1960 issue of the Proceedings of the Entomological Society of Washington. Thus, his life-long hobby and one-time vocation provided him with an active and much-needed interest as well as an opportunity to remain a part of the world fraternity of entomologists until the final year of his life.

An early sidelight of his life was his association with John J. Pershing, who was ROTC instructor at the University of Nebraska in 1893. At this time Mr. Barber was one of the group of students that organized a drill team that became the first Chapter of the National Honorary Society known as the Pershing Rifles, and at the outbreak of the Spanish-American War, Pershing asked him to serve as adjutant of the cavalry regiment he was to command in the Cuban campaign. One cannot but wonder what fortune and circumstance would have been in store for Mr. Barber had this quiet, scholarly man chosen to take up a military career as a member of the staff of "Black Jack" Pershing.

Although the Barbers had no children, they reared Mrs. Barber's younger brother, Richard, and through their contacts in later years with Mr. Barber's more youthful colleagues, they enjoyed an almost parental relationship with a generation of the younger hemipterists and other entomologists.

His character was marked by tolerance of views not coinciding with his own. He stated his opinions clearly and forcefully, but never attempted to impose them upon others. Moderation was reflected in all aspects of his life. These characteristics were without doubt responsible for the high regard in which he was held by his colleagues, many of whom are sons of a generation not yet born when his entomological career began.

MORTIMER D. LEONARD
REECE I. SAILER

Horace F. Barnes
1902-1960

The unexpected and unfortunate death of H. F. Barnes on Feb. 5, 1960, has removed from entomological circles one of the world's outstanding proponents of bio-systematics, and from human companionship a heartwarming gentleman.

Dr. Barnes was born at Bedford, England, where he spent his boyhood and received his grammar school education. In 1921 he responded to an interest in zoology by attending Queen's College, Oxford, where he was awarded a B. A. degree. Three years later he moved to Wye College (University of London), where he started his world-famous study of gall midges under the late F. V. Theobald, with the aid of a graduate scholarship from the Ministry of Agriculture. He received his Ph.D. there in 1928.

He spent the 33 years between 1927 and the time of his death as a member of the research staff of the Entomology Department, Rothamsted Experimental Station, Harpenden, Hertsfordshire, performing some of the most fruitful biological investigations ever to emerge from the study of Diptera. His keen interest in the gall midges (Cecidomyiidae) led him to explore a wide range of biological phenomena which included parasitism and predation, plant resistance to cecid attack and other host-insect relationships, and many features of bionomics such as emergence and sex ratios. He was particularly interested in cecids from the viewpoint of the host attacked—many of his papers reflect this position by presenting the available information about all of the species inhabiting a host species or species group. His

HORACE F. BARNES

efforts in this direction culminated in a seven-volume series (the eighth and final one incomplete and unpublished) about the gall midges of economic importance. Each of these volumes covers a separate broad classification of plants (e.g., Vol. 1, Root and Vegetable Crops; Vol. 2, Fodder Crops; etc.) and contains recent control and taxonomic as well as biological information. Among his best known works are the studies of the fluctuations of insect populations, based on researches on cecids in Broadbalk wheat, and his successful and significant crossings of hessian fly from Italy, Germany, England, and the United States.

H. F. Barnes, although primarily not a cabinet systematist and hence not particularly interested in taxonomic categories above the generic level, had an "eye"

for morphological species—descriptions of new ones are scattered throughout his bibliography. This ability was especially fortunate, for he was thus enabled to incorporate morphological and biological data into a system of bio-systematics which his successors will do well to emulate and promote. His magnificent collection of about 15,000 slides is now in the care of the British Museum (Natural History).

Dr. Barnes made two trips to the United States. The first of these, at about the time he joined the Rothamsted staff, was to visit E. P. Felt at the New York State Museum. This meeting was fortunate—Barnes beginning a fruitful career, Felt at the peak of his authority on the North American gall midges. The visit made a lasting impression, for when Barnes returned for a second time in the late summer of 1956, he often spoke of that association as ". . . all too brief." It was in 1956 that the writer became infected with Barnes' enthusiasm for biosystematics and his intense interest in all living things. Barnes visited agricultural research centers and delivered several lectures throughout the eastern half of the United States in addition to working at a microscope at the U. S. National Museum during his second visit.

Dr. Kenneth Mellanby writes, ". . . His enthusiasm for research never flagged. Weekends and holidays were never allowed to interrupt his work, and he would devote his time to helping and instructing visiting scientists even when this meant that his own experiments would keep him at work until late into the night, for he never went home until his work was finished." In 1958 his outstanding contribution was recognized by special promotion to the rank of Senior Principal Scientific Officer—a promotion uncommon among research workers who have not strayed into administration.

Some of his other interests included a study of slugs, to which he devoted much of his spare time, the editing of the *Bedfordshire Naturalist*, and serving as treasurer of the Association of Applied Biologists. He was a member of the Entomological Society of America from 1927 to 1937 and a Fellow from 1937 to 1951.

In addition to his wife and a daughter, Janet Barnes, he is survived by two sons who have inherited his love and concern for science: R. F. Barnes is a Lecturer in Plant Pathology, I.C.T.A., Trinidad; and T. R. Barnes is an Agricultural Officer in Nigeria.

RICHARD H. FOOTE,
Entomology Research Division,
U. S. Department of Agriculture

BOOK REVIEW

TICKS. A MONOGRAPH OF THE IXODOIDEA. PART V. On the genera *Dermacentor*, *Anocentor*, *Cosmiomma*, *Boophilus*, and *Margaropus*, by DON R. ARTHUR. New York: Cambridge Univ. Press, 1960, xviii+251 pp. Illus. $11.50.

This classic series of monographs was initiated by G. H. F. Nuttall, C. Warburton, W. F. Cooper and L. E. Robinson in 1908 with the publication of Part I dealing with the Argasidae. Part II (Ixodidae, the genus *Ixodes*) by Nuttall and Warburton, plus a companion Bibliography of the Ixodoidea by Nuttall, Robinson and Cooper, appeared in 1911. Part III (the genus *Haemaphysalis*) by Nuttall and Warburton was published in 1915 and Part IV (the genus *Amblyomma*) by Robinson in 1926. Now, 34 years later, publication of the series is resumed with Part V under the authorship of Dr. Arthur of the University of London, with announcement that Parts VI, the genera *Rhipicephalus* and *Rhipicentor*, and VII, the genus *Hyalomma* are planned.

The major portion of this volume deals with the 11 species of *Dermacentor* recognized for North and Central America, 15 species and 1 subspecies for Eurasia, and 2 species and 1 subspecies for Africa, plus an annotated list of 25 species referred to as condemned, doubtful, insufficiently described or based on insufficient material. Following the generic description, some 30 pages are devoted to a detailed and well-illustrated morphological study which, according to the author, is to serve as a background to systematic studies. Treatment of species is according to the geographical basis indicated above and includes keys to males, females, and immature stages when known. Under the species in this and the other genera treated is a section on Synonymy, Literature, and Iconography. This is followed by descriptions, and additional information is provided under headings such as Remarks, Related Species, Biology, Economic Importance, Disease Relationships. Most of the species throughout the volume are well illustrated by drawings and good photographs of some of the Dermacentors are included.

The genera *Anocentor* and *Cosmiomma* each contain but 1 species, *nitens* (Neumann) of the New World and *hippopotamensis* (Denny) of Africa, respectively.

Dr. Arthur follows present trends in recognizing only 3 species in the genus *Boophilus*, *annulatus* (Say), *microplus* (Canestrini) and *decoloratus* (Koch), and in discarding Minning's subgenera *Uroboophilus* and *Palpoboophilus*. Two species, *Palpoboophilus minningi* Kishida 1936 and *P. brachyuris* Kishida 1939 have not been included. It is of interest to note here the recent discovery of a new species in Palestine by Hoogstraal and Kaiser, the description of which appeared shortly after the publication of the present volume.

Two species are included in *Margaropus*, *winthemi* Karsch and *reidi* Hoogstraal, both of which are African. This section is taken very largely from Hoogstraal's 1956 comprehensive work on the ticks of the Sudan.

Few taxonomic changes have been made. *Conocentor* Schulze 1943 is reduced to a synonym of *Dermacentor*, and oddly enough this is done in the review of the synonymy of the type species *D. everestianus* Hirst rather than in the synonymy of *Dermacentor* itself. *D. birulai* Olenev is synonymized under *D. everestianus*, and *D. birulai kukunoriensis* Olenev appears as a synonym of both *D. nuttalli* and *D. everestianus*! The author concludes that *D. daghestanicus* Olenev is a synonym of *D. niveus* Neumann. Because of the earlier established synonymy of *D. variegatus* Marx and Neumann under *D. albipictus* (Packard), *variegatus* var. *kamshadalus* Neumann of Kamchatka is uncritically accepted as a subspecies of *albipictus*. In doing so, the elevation of *kamshadalus* to species rank by Serdyukova in 1955 apparently has been overlooked.

The only new species included in the work is *D. asper*

"(Chinese form)" which is described without additional information as to origin of the 2 males on which it is based. Evidently the author regards it as a "variety" of *D. reticulatus*. No figures are given.

Dr. Arthur has done a great service in bringing together in one volume a vast amount of information. The keys, descriptions and illustrations are for the most part good, as is the section devoted to morphology. However, this volume does not attain the standards of excellence set by the earlier parts of this monographic series. For a better understanding of the genera treated, a key to the genera of the Ixodidae would have been helpful to the nonspecialist. In several instances literature references to genera are unaccountably placed under species and vice versa. Although the synonymy of the several genera and species treated is complete or nearly so, the same cannot be said for references to Literature and Iconography, many important papers in these categories having been overlooked or omitted, *e.g.*, only 3 listed for *B. decoloratus* (p. 214). Distributional data presented are woefully inadequate for several species, inaccurate for some including *D. albipictus*, *D. parumapertus*, *D. hunteri*, *D. latus* and others, and totally lacking for *D. raskemensis* and *Margaropus winthemi*. Many important references to biologies are omitted though less significant ones are cited. Disappointing also is the meager and frequently undocumented information provided on disease relationships, which hardly accords with the introductory statements (p. 1) as to the "immense medical and economic importance to both man and his domestic stock" of various species of *Dermacentor*. The classic Smith and Kilbourne reference to transmission of Texas fever by *Boophilus* is not even cited.

Many additional errors, omissions, and inconsistencies, minor or otherwise, in this volume also detract from its value as a textual reference. To cite but a few noted in only the first 3 chapters—p. 6, *D. antrorum* should have been mentioned as another exceptional species in which coxae I–IV do not increase progressively in size, also *Pseudixodes* misspelled; p. 8, *maculatum* misspelled; p. 40, parentheses around Say following *Dermacentor variabilis* omitted; p. 42, scales of magnification obviously inaccurate in figures here; p. 44, fig. 60, shape of coxa IV atypical; p. 45, fig. 69 inverted; p. 50, male of *D. parumapertus* said to be only very slightly ornate but on p. 51 color pattern is said to be extremely variable, ranging from complete absence to extensive ornamentation. It is rather startling to read, p. 54, that the author considers *D. parumapertus* "an extraordinarily Rhipicephalid-like species", and that "the shape of the basis capituli and the enlarged coxa IV of the male are almost the only characters inconsistent with that genus", when these are in fact major characters distinguishing the two genera. Hosts of adults other than rabbits are not mentioned, p. 56, though several have been recorded. One is led to believe that cattle are the important if not the only hosts of the immature stages of *D. occidentalis* (p. 63) though in 1937 the reviewer reported their occurrence on several species of rodents and other animals. Disease relations of this important species are not discussed at all, and the species is not even mentioned in the cited 1932 paper by Rees. Under *D. andersoni*, p. 74, the Marx 1892 paper is not listed in the References, and numerous important papers dealing with this species are not mentioned. The statement, p. 84, that "geographical areas affected with paralysis do not produce the Rocky Mountain spotted fever" is of course erroneous. No documentation is given in the discussion of the biology of *D. albipictus*, the well-known winter tick of North America which the author calls the "red-brown tick", p. 92. A great deal more could have been said about disease relationships of this important tick. Under *D. dispar*, p. 98, the scientific name of the peccary is misspelled, and figure 185, p. 101, is of *dispar* and not of *latus* as labelled. Fairchild's 1943 report in which *D. latus* is recorded for Panama is not cited, though listed in the References where the author's name is misspelled.

Despite its shortcomings, this book will be welcomed by all who are interested in ticks. However, the author and editor would have done well to have had the manuscript reviewed by competent specialists, and it is hoped they will do so if Parts VI and VII are undertaken as planned.

GLEN M. KOHLS
Rocky Mountain Laboratory
U. S. Public Health Service

INDEX XVI
INDEX TO THE LITERATURE OF AMERICAN ECONOMIC ENTOMOLOGY

Number XVI of this series, which was published in 1959, covers the literature for 1956 and 1957. The book contains 704 pages. Indexes I through XV covering the literature from 1905 through 1955 are also available.

Index XVI is bound in black buckram as are previous volumes. Helene G. Cushman, the Compiler of Index XVI, has carried on the high tradition of excellence set by her predecessors.

Price postpaid $6.00; to E.S.A. members $4.00

Order from
ENTOMOLOGICAL SOCIETY OF AMERICA
4603 Calvert Road
College Park, Maryland

INDEX TO VOLUME—53

All new names are printed in *italics*

Abroteles, 826
Acanthocera *bequaerti*, 3
Acari, 293
Acarina, 27, 35, 183, 251, 848
  ecology of, 67
Acaronychus traghardi, 252
Acarus siro, 549
Acerentomon, 676
Acerentomonidae, 675
Acetate, 1-C^{14}, utilization by Musca domestica, 128
Acheta assimilis, 721
Achipteria, 251
Achorutes
  nothus, 76
  spp., 68
Aciurina notata, 254
Acoenoniini, 312
Acrididae, 441
Acrocera n. sp., 849
Acroceridae, 416
Acromyrmex, larvae, 109
Acroneuria pacifica, 714, 717
Aedes aegypti, 467, 689
  adults, longevity and productivity factors, 277
  postemergence changes of enzyme activity in, 86
Aedes
  (Stegomyia) aegypti, eggs, 13
  (Ochlerotatus) atlanticus, eggs, 17
  (Finlaya) atropalpus, eggs, 14
  cantator, eggs, 17
  dorsalis, breeding in Nevada, 706
  (F.) hendersoni, restoration of name, 600
  hendersoni complex, 604
  (O.) infirmatus, eggs, 17
  melanimon, breeding in Nevada, 706
  (Taeniorhynchus) mitchellae, eggs, 16
  nigromaculis, 689, 706
  (T.) sollicitans, eggs, 16
  (T.) taeniorhynchus, eggs, 16
  (O.) thibaulti, eggs, 17
  triseriatus, 601
  vexans, 706
Aeschna multicolor, 729
Agabus lugens, 423
Agkistrocerus
  finitima, 365
  megerlei, 365
Agria affinis, 97
Agrionidae, 439
Agromyzidae, 130
Agrosoma, new genus for Tettigonia pulchella, 18
  akenalis, 22
  bispinella, 25
  carinona, 22
  cruciata, 25
  decepta, 24
  exukanis, 24
  glyphalis, 24
  placetis, 24
  proxima, 25
  pulchella, 22
  syklis, 22
  terebra, 24
Agulla, 716
  adnixa, 718, 721, 726
Alabama argillacea, light trap sampling, 525
Aleuroglyphus ovatus, 549
Algae in Wisconsin streams breeding black flies, 390
Ali-esterase activity in Musca domestica, 360
Alistruma, larvae, 109
Alkali bee (see Nomia melanderi, 425)
Allomerus, larvae, 109
Alloxysta spp., 405
Ametastegia glabrata, 665
Amino acids
  in egg shell of Drosophila melanogaster, 170, 732
  aminopolysaccharides, investigation of, 732
  of sperm of Apis mellifera, 841
Amiota, 133, 134
Amphasia interstitialis, 69
Amphimallon majalis, vertical distribution of, 666
Anagasta sp., 770
Anajapygidae, in North America, 575
Anajapyx, 575
  amabilis, 578, 583
  hermosus, 578, 583
  menkei, 576, 582
  mexicanus, 575, 583
  vesiculosus, 576, 583
Ancistrocerus tigris tigris, 849
Anergates, larvae, 109
Angelothrombium pandorae
  biology of, 293
Anisoptera, 851
Anobiidae, ecology of, 71
Anopheles quadrimaculatus, 459
  anatomy of larval alimentary canal and mouthparts, 459
  larval feeding behavior, 464
Anthonomus, identification of
  grandis, 548
  grandis thurberiae, 548
Anthribidae, ecology of, 72
Antillocoris minutus, 318
Antipaluria aequecercata, 718
Aonidiella aurantii, 701
Aoplus sp., 571
Apanteles
  cingiliae, 566, 571
  enypiae, 566
  militaris, 665
  paleacritae, 566, 572
  sp., 665
Apatolestes
  albipilosus, 365
  comastes, 364
    fulvipes (var.), 364
    willistoni (var.), 364
  villosulus, 364
Aphaenogaster, larvae, 109
Aphaereta
  auripes, 197
  pallipes, 197
Aphelinidae, 701
Aphelinus semiflavus, 144, 158
Aphid hosts of California parasites, 412
Aphidae, 735
Aphidencyrtus aphidivorus, 405
Aphidiinae, 144, 149, 404
  parasitic spp. attacking aphid hosts in California, 413
Aphidius
  (Aphidius) alius, 405
  (Lysiphlebus) chrysoaphidis, 407
  (Aphidius) confusus, 405
  (A.) nigripes, 406
  (A.) nigriteleus, 406
  (A.) ohioensis, 406
  (A.) pisivorus, 406
  (Protaphidius) ponderosae, 407
  (Aphidius) pterocommae, 407
  (A.) ribis, 407
  sp., perhaps obscuripes, 848
  (L.) testaceipes, 159, 408
Aphis medicaginis, feeding preferences among Melilotus sp., 696
Aphytis spp., parasites of red scale, 701
  chrysomphali group, 704
  coheni, 701, 705
  fisheri, 704
  holoxanthus, 701, 704
  immaculatus, 704
  lingnanensis, 704
    parasite of Aonidiella aurantii, 701
    parasite of Chrysomphalus aonidum, 702
  melinus, 704
  mytilaspidis group, 704
Apis mellifera, 618
  dietary requirements, 618, 695
  longevity as affected by diet, 620
  separation of seminal plasma and sperm amino acids of, 841
Apoidea, 809
Apterostigma, larvae, 109
Araneida, 67, 848
Arctopsyche grandis, 724
Argas, 611, 625, 743
  brevipes, 631
  brumpti, 446
  (A.) *cooleyi*, 625, 750
  columbarum, nomen nudum for A. reflexus, 611
  disease relationships, 754
  distribution and hosts, 617, 631, 753
  (A.) persicus, 446, 611, 750
  (A.) reflexus, 617, 625, 743
    complex, 611
  (A.) reflexus group, 611, 617
    hermanni, 617, 743

lagenoplastis, 754
reflexus, 611, 631, 743
spp. and sub spp., 446
Argasidae, 446, 611, 625, 743
Arge clavicornis, 722
Argidae, 722
Armyworm (see Pseudaletia unipuncta)
Arphia pseudonietana, 514
Arthropods, list of, found in empty cocoons of Diprion similis, 848
Asaphes
californicus, 405
fletcheri, 405
vulgaris, 159
Asilidae, 328
Aspididris, larvae, 109
Aspidiotus hederae, factitious host of Aphytis spp., 702
Astega spp. (see Cnephia, 213)
Astigmatophthalmus, 366
Atractodes sp., 197
Atrichomelina pubera, 192
immature stages, 192, 197
parasites reared from, 197
Atta, larvae, 109
Atylotus
duplex, 366
incisuralis, 366
thoracicus, 366
tingaureus, 366

Bactridium convexulum, 70
Barnesina, 305, 314
hylecoites, 315
quercivora, 315
Basidiomycetes, 61
Bayer 22408, against eye gnats, 537
Bayer 29493, against eye gnats, 536
Bdella sp., 67
Bees, ground-nesting, use of Bio-plastic in excavation of burrows, 679
Beetles, desert water
colors of, 422
distribution range, 423
Sonoran spp., 422
Beetles, excretion products in stored-grain, 632
Belba sp., 67
Berosus, 423
Bessa harveyi, 476
Bidessus, 424
obtusus, 423
(sensu latus), 422
spp., 423
spretus, 423
Biluna, oriental subgenus of Xylocopa, 809
Biological control
importance of taxonomy to, 701
of Aonidiella aurantii, 701
of Chrysomphalus aonidum, 701
Biology of
Angelothrombium pandorae, 293
aphid parasites, Pacific Coast, 404
Argas (A.) reflexus hermanni, 743
(A.) persicus, 743
Atrichomelina pubera, 192
Caminella peraphora, 31
Ceratopogonidae, Cactiphilic species, 659
Cnephia jeanae, 219
Dinothrombium, 293
Enypia at various stages, 561
giant red velvet mites, 294
Heterosylum robustum, 425
Hyalomma aegyptium, 457
Lyctus planicollis, 285
Omalus, 235
Omania from Samoa, 494
Pachypsylla celtidis-gemma, 265
Polistes in North Carolina, 111
Praon palitans, 144
ticks (Ixodoidea) of Lybia, 445
Trichoplusia ni, 229
Bittacus pilicornis, 721
Blaberus
craniifer, 80, 492
giganteus, 80
Black flies of Wisconsin, immature stages, 386
parasites and predators, 392
population densities, 387, 392
species infested with nematodes, 397
Blatta orientalis, 80
Blattaria, 716, 720, 722
Blattella
germanica, 80, 714
lituricollis, 80
vaga, 80
Blattella germanica
distinguishing sexes in early nymphal stages, 550
ultrastructure of heart, 369
Bledionotinae, 319
Blissinae, 320
Blissus leucopterus, 320
Boletotherus cornutus, 67, 69, 71, 77
Bolivaridinae, 675
Boll weevil (see Anthonomus grandis)
Bombyliidae, 425
Bombylius, parasite of bees, 429, 433
Bombyx, 608
Book Reviews: Authors:
Arthur, Don R., 855
Christophers, Sir Rickard, 546
Dennis, Clifford J., 182
DuPorte, E. M., 283
Hardy, D. Elmo, 762
Haupt, Hermann, 808
Leston, D., 442
Murachi, E. K., 670
Schmutterer, H., 191
Southwood, T. R. E., 442
Tokunaga, Masaaki, 670
Wigglesworth, V. B., 554
Book Reviews: Titles:
Aëdes aegypti (L.) the Yellow Fever Mosquito, Its Life History, Bionomics, and Structure, 546
Die Tierwelt Deutschlands 45. Coccoidea I. Diaspididae, 191
Diptera: Nematocera—Brachycera, 762
Elemente Einer Systematischen Aufteilung der Macromerinae, 808
Insects of Micronesia. Diptera: Ceratopogonidae, 670
Laboratory Manual for Introductory Entomology, 182
Land and Water Bugs of the British Isles, 442
Manual of Insect Morphology, 283
The Control of Growth and Form: A Study of the Epidermal Cell in an Insect, 554
Ticks. A Monograph of the Ixodoidea. Part V. On the genera Dermacentor, Anocentor, Cosmiomma, Boophilus, and Margaropus, 855
Boophilus annulatus, 448, 455
Brachyneura, 306
Brachyneurini, 306
Braconidae, 144, 197, 404, 542, 566, 571
Brephometra (=Pero=Meinertomyia), 306
Brevicoryne brassicae, increase on treated cabbages, 203
Brittenia, 305, 313
Bulbitermes, 828
Byrsotria fumigata, 80

Cacoxenus
indagator, 356
inquilinus, 554
Calcium oxalate in oöthecae of cockroaches, 79
Callachna, 671
gibba, 254
Calliphoridae, 553
Caloglyphus berlesei, 549
Caminella peraphora, 27
Caminellinae, 27
Camisia biverrucata, 252
Camnula pellucida, 520
Campodeoidea, 575
Camptoptera pulla, 74
Cantharidae, 726
Carabidae, ecology of, 69
Cardiocondyla, larvae, 109
Carebara, larvae, 109
Carpenter bees, bamboo-nesting, New World subgenus of Xylocopa, 809
Carpilis consimilis, 318
Casca smithi, 702
Casinaria
geometrae occidentalis, 566
eupitheciae, 571
Cataulacus, larvae, 109
Catochini, 307
Catotrichini, 306
Cecidomyiidae, 73, 305
Celtis trees, effect of gall formation see Pachypsylla celtidis-gemma)
Cemonus (See Pemphredon)
Cephalotes, larvae, 109
Cepheus, 252
Ceracis sp., 70
Ceraphronidae, 405
Ceratina, host of Omalus, 235
Ceratochaeta tortricis, 97
Ceratomyia, 306
Ceratopogonidae, from cacti, 639, 659
Ceromasia auricaudata, 97
Chaetophlepsis
semiothsae, 566, 572
sp., 572
Chaetostoma, 255
Chalastogastra, 510
Charips spp., 405
Chastomera, 306
Chauliognathus marginatus, 726
Chauliopinae, 320
Chiggers of Guatemala, 183
Chilopoda, ecology of, 68
Chloropidae, 134
Chlorotabanus
(Cryptotylus) chloroticus, 5
(C.) inanis, 5
(C.) mexicanus, 5
(Cryptotylus) unicolor, 5
Cholesterol 4–C^{14}, utilization by Musca domestica, 260
Cholinesterase activity in Musca domestica, 360
Choristoneura fumiferana, dipterous parasites of, 84
Chorizagrotis auxiliaris, oviposition by, 474

Chortippus longicornis, 436
Chromolepida, 161
Chrysididae, 235
Chrysomelidae, ecology of, 72
Chrysomphalus aonidum, 701
Chrysopa sp. ploribunda group, 849
Chrysops
  auroguttata, 2
  bulbicornis, 3
  formosa, 3
  incisa, 7
  laeta sublaeta, 3
  pallidefemorata, 3
  tristis, 2
  variegata, 2
Chymomyza procnemis, 133, 136
Cicada, 730
Cicadellidae, 18, 843
Cinara sp., 849
Cisidae, ecology of, 70
Cissites, parasite in bees' nests, 817
Clarkistruma, larvae, 109
Clausenia purpurea, 705
Cnemodus movartius, 318
Cnephia
  borealis, 213
  dacotensis, 219
  (Cnephia) dacotensis, 387
  freytagi, 216
  jeanae, 218
  lapponica, 213
  (Stegopterna) mutata, 387
  pecuarum, 213
  saileri, 213
  sommermanae, 213
  sp. #1 and sp. #2, 395
  (Ectemnia) taeniatifrons, 398
  villosa, 213
Coccinellidae, ecology of, 71
Coccophagus lycimnia complex, 384
Coccus
  hesperidum, 384
  primary parasites of, 384
  pseudomagnoliarum, 385
Cockroaches
  calcium oxalate in oöthecae, 79
  nucleic acids in, 491
Coelopidae, 134
Coleoptera, 8, 280, 548, 584, 717, 726, 825, 848
  ecology of, 69, 73
Collembola, 481
  ecology of, 68
Colydiidae, ecology of, 70
Constrictotermes, 825
Coptotermes
  acinaciformis, 834
  lacteus, 834
Coptotermoecia
  aluticia, 834
  gayi, 834
Corethra, 467
Corotoca, 826
Corotocini (Aleocharinae), 825
Corrodentia, 68, 848
Coruna clavata, 405
Cossidae, 726
Cowpea aphid (see Aphis medicaginis)
Crematogaster, larvae, 109
Cryphula parallelogramma, 318
Cryptolestes
  ferrugineus, 10, 632
  minutus, 10
  turcicus, 11, 632
Cryptophagidae, ecology of, 70
Cryptophagus sp., 70
Ctenacroscelis mikado, 721
Cucujidae, 8, 70
Culex, 467
Culicidae, 11, 134, 459, 600
Culicoides, Copiosus group, 639, 646, 648, 661
Culicoides, 652, 657, 660
  arizonensis, 655, 660
  bakeri, 652
  borinqueni, 658, 661
  butleri, 650
  cacticolus, 653, 660
  copiosus, 657, 660
  hinmani, 658, 661
  insolatus, 654, 660
  jamaicensis, 649
  jonesi, 650, 660
  loughnani, 649
  panamensis, 649
  pilosus, 648
  poikilonotus, 648
  propinquus, 648
  ryckmani, 656, 660
  sitiens, 652, 660
  torridus, 654, 660
  wirthomyia, 639
Cunaxa, 322
  boneti, 324
  capreolus, 324
  setirostris, 324
  simplex, 324
  taurus, 322
  womersleyi, 324
Cunaxidae, in Florida, 321
Cunaxoides, 322
  andrei, 324
  croceus, 324
  pectinatus, 326
  pectinellus, 324
Curculionidae, 548
Cybister, 423
Cymberemaeus, 251
Cynipidae, 405
Cyphomyrmex, larvae, 109

Daceton, larvae, 109
Dacryon, larvae, 109
Dahlbominus fuscipennis, 849
Dasineura, 306
Dasychela, 365
Dasyhelea, 639
  cactorum, 642, 660
  pentalineata, 642, 660
  ryckmani, 646, 660
Dasyheleinae, 642
DDVP, against eye gnats, 537
Dermaptera, 716, 720
Deronectes, 422
  aequinoctialis, 423
  spp., 423
  striatellus, 423
Desmopachria, 422
Diachlorus
  bicinctus, 3
  badius, 368
  curvipes, 3, 368
  ferrugatus, 368
  jobbinsi, 368
  scutellatus, 3
Diaeretus
  rapae, 409
  salicaphis, 409
Diapriidae, undetermined sp., 197
Diatoms in Wisconsin streams breeding black flies, 390
Dibrom, against eye gnats, 537
Dicapthon, against eye gnats, 537
Dichelacera ochracea, 3
Dichothorax, larvae, 109
Dicladocera, 365
Dictenulus, 236
Dilobocondyla, larvae, 109
Dimethoate, against eye gnats, 537
Dinothrombium, 293
  insulare, 294
  tinctorium, 294
Diodontus, host of Omalus, 235
Diplocardia communis, 553
Diplopoda, ecology of, 68
Diploptera punctata, 80
Diplorrhos, 236, 245
Diplura, 137, 575
Diprionidae, 510
Diprion similis
  empty cocoons as habitat niches for arthropods, 847
  sex attractant in, 510
Diptera, 1, 11, 73, 121, 130, 133, 160, 192, 213, 253, 305, 328, 356, 386, 416, 425, 459, 476, 513, 553, 572, 600, 639, 659, 665, 671, 721, 848
  reared from snails
    Atrichomelina, 192
    Ephydridae, 197
    Piophilidae, 197
    Phoridae, 197
    Sarcophagidae, 197
Discourellinae, 30
Drosophila, 133, 170, 174
  flavopinicola, 136
  hydei, 136
  melanogaster, 134
    description of egg, 170
    larval activities, 178
    origin of strains, 175
  nanoptera, 136
  neocordata, 135
  parasaltans, 136
  pseudoobscura, 134
  repleta, 134
  setula, 136
  subsaltans, 136
  thoracis, 136
  victoria, 134
  virilis, 134
Drosophila melanogaster
  chemical components of egg shell, 170, 732
  factors affecting pupation sites, 174
Drosophilidae, 133, 356
  ecology of, 73
  repleta group, 659
Drymus unus, 318
Dusona
  pilosa, 566
  luctuosa, 566
Dylox, against eye gnats, 537
Dysdercus cingulatus
  embryonic cuticles, 538
  endocrine system, 540
Dytiscidae, 422

Earthworms used in larval feeding of Pollenia rudis, 553
Eburniola, 826
Ecology of
  Aedes hendersoni and A. hendersoni complex, 604
  A. triseratus, 604
  Ceratopogonidae in cacti, 659
  desert water beetles, 422
  Enypia, 560
  immature stages of black flies, 386
  inhabitants of woody shelf fungi, 61

Megalonotinae, 318
Oribatid mites, 251
Pollenia rudis, 553
ticks of Lybia, 445
Ectobius
pallidus, 89
panzeri, 80
sylvester, 80
Elampinae, 235
Elampus, 235
Elateridae, ecology of, 70
Embioptera, 714, 718
Enallagma exsulans, oviposition of, 439
Encyrtidae, 405
Eniochthonius (Hypochthoniella), 252
Ennearthron sp., 70
Entomobrya, 482
Entomobryidae, 481
Enypia, revision of genus, 560
coolidgi, 572
griseata, 568
moillietti (see griseata, 568)
packardata, 571
perangulata (see venata, 561)
venata, 561
Eosentomonidae, 675
Ephemeroptera, 714, 729
Ephredus
californicus, 409
nitidus, 410
Ephydridae, 134, 197
Epicauta spp., 696
Epidoseini (see Porricondylini)
Epilachna varivestis, effect of light on temperature preferendum of larvae, 591
Epilohmannia, 252
Epimyia, 306
Epiophlebia, 716
Epomyia, 160, (see Furcifera)
bella, 161, 164
pictipennis, 161
Epopostruma, larvae, 109
Epourenia viva, 306
Equipment
eye-gnat trap and olfactometer, 530
Eremaeus, 252
Eremocoris ferus, 318
Eretes sticticus, 423
Erythraeus sp., 848
Esenbeckia prasiniventris, 1
Euaresta bellula=stelligera, 254
Eubadizon orchesiae, 73
Euglossa, 818
Euleia, 255
Eulonchus, 416
halli, 418
marginatus, 416
marialiciae, 416
sapphirinus, 416
smaragdinus, 416
group, 416
pilosus, 418
smaragdinus, 417
tristis, 416
Eulophidae, 566
Eumea caesar, 97
Euneura lachni, 405
Euparius marmoreus, 70
Eupelmella dryorhizoxeni, 849
Eupelmus
allynii, 724
sp., 849
Euphorinae, 542
Euphycus, 161
Euphytomima nomiavora, 426
Euplectrus mellipes, 566
Euribia cardui, 254
European chafer (see Amphimallon majalis)
Eurycotis floridana, 80
Euschöngastia
desmodus, 188
libertatis, 189
nuñezi, 190
precaria, 190
Eusimulium, 386, 400
aureum, 398
aureum complex, 387
croxtoni, 399
gouldingi, 399
johannseni, 399
latipes, 399
pugetense, 400
Eustalocerus clavicornis, 542
Eutreta baccharis, 254
Eutrombidium, 294
Evalljapyx, 137
adonis, 142
anombris, 138
macswaini, 142
newelli, 140
ombris, 140
sonoranus, 143
Exorista melba, 665

Fannia canicularis, 665
Fidenia *trinidadensis*, 1
Fitch, Asa, writings of, 326
Fonsecia anguina, 186
Forcipomyia, 639
christiansoni, 640, 660
cinctipes, 642
desertensis, 639, 660
townesi, 640
varipennis, 642
Forellia onorpordi, 254
Forficula sp., 718, 720
Formicidae, 793
Frirenia, 305, 313
Fruit flies (vinegar flies), damage to tomatoes by egg deposits, 170
Fucomyia vanduzeei, 134
Furcifera, 160
achaeta, 169
bella, 167
braziliana, 166
diversipes, 166
fascipennis, 165
flavipes, 166
fulvipennis, 166
hardyi, 167
kröberi, 169
longicornis, 165
pictipennis, 167
polita, 166
rufiventris, 168
scutellaris, 168
sumichrasti, 168
underscribed spp., 167
Furcifera-Epomyia complex, 161

Galleria, effect of injury on oxygen consumption by pupae, 850
Galleria mellonella, 697
foregut activity in larvae of, 346
Galumna, 252
sp., 67
Gastropoda, ecology of, 67
Geocorinae, 320
Geocoris
ulighinosus, 320
bullatus, 320
Geometridae, 560
Gerridae, 729
Giant red velvet mites, 293
Gioliella, 306
Gitona, 356
Gitonides perspicax, 356
Glischrochilus sp., 70
Glyptoscelis sp., 849
Gnophomyia tristissima, 722
Grallatotermes, 828
Grasshoppers
egg production and mortality, 518
extended diapause in eggs of high-altitude species, 436
parasites on, 294
suppression by Nemestrinid parasties, 513
Gryllidae, 729
Guatemala, chiggers of, 183
Gymnophthalma interrupta, 97
Gypsy moth, 686

Habrocytus thyridopterigis, 849
Hackberry gall-former, life cycle of, 265
Haemaphysalia punctata, 454
Haemaphysalis otophila, 448, 455
Halictus, host of Heterostylum
farinosus, 434
rubicundus, 426
Hamatabanus, 365
annularis, 365
carolinensis, 365
sexfasciatus, 365
Haplothrips, 507
?clarisetis, identification of, 507
cottei, 508
distalis, 508
fasciculatus, 508
faurei, 508
graminis, 508
halophilus, 508
malifloris, 508
Haplusia, 306
Haplusiella, 306
Hatching stimulus for Aedine mosquito eggs, 688
Hedychridium, 235
Hedychrum, 235
Heleidae (see Ceratopogonidae)
Heliothis zea
morphology of reproductive system, 763
percentage of mating, 779
Heliothis, pupae of
virescens, 551
zea, 551
Helodrilus
caliginosus, 553
chloroticus, 553
foetidus, 553
roseus, preferred food of Pollenia rudis, 553
Hemerobius sp., 849
Hemimetabola, 717
Hemiptera, 68, 317, 538, 691, 728, 848
Henesterinae, 320
Hepialidae, 726
Herbicide 2,4-D, effect on pea aphids, 199
Hermannia, 251
Hesperentomon macswaini, 676
Hesperentomonidae, of Protura, 676
Heterometabola, 606
Heteropeza, 305, 310
pygmaea, 310

ulmi, 311
Heteropezina cathistes, 311
Heteropezinae (see Cecidomyiidae)
Heteroptera, 317, 494, 606, 728
Heterostylum, parasite of bees
englehardti, 426
robustum, biology of, 425
sp., larvae of, 431, 433
Hierodula patellifera, 720
Hippelates, attractancy of
proteinaceous materials to, 835
attractancy as affected by aging of materials, 836
concentration of materials, 840
attractants emanating from insects, 839
baits and chemical attractants against, 529
collusor, 530, 835
dorsalis, 530, 835
hermsi, 835
pusio, 530, 835
robertsoni, 530, 835
Holometabola, 606, 717
Holopyga, 235
Homoptera, 18, 68, 265, 728, 735, 843, 848
Honey bee (see Apis mellifera)
Honeydew of Myzus persicae, 220
Hoplophora magna, 251
Hoplothrips
angusticeps, 69
major, 69
House fly (see Musca domestica)
Hulsantina picta, 848
Hyalomma (Hyalomma)
anatolicum
anatolicum, 449, 455
excavatum, 450, 455
subspp. intermediate, 450
dromedarii, 450, 455
franchinii, 450
impeltatum, 451, 455
marginatum, 451
rufipes, 451, 455
turanicum, 455
spp., 451, 454
Hyalomma (Hyalommasta) aegyptium
host relationships, 457
parasites of tortoises in Turkey, 457
Hybomitra, 6
astuta, 366
lapponica, 366
sexfasciata, 366
typha, 366
Hydrocanthus spp., 424
Hydrophilidae, 422
Hydroporus, 422
kingi, 423
lapponum, 422
sp., 422
Hylaeus, host of Omalus, 235
Hylemyia fugax, 665
Hymenoptera, 73, 111, 144, 197, 235, 384, 404, 476, 510, 542, 566, 571, 572, 665, 701, 717, 722, 793, 809, 848
Hyperparasites, 405
Hyperparasitism, 158
Hypochthoniella (see Eniochthonius)
Hypogeocoris piceus, 320
Hyposoter
annulipes, 665
basizona, 566

Ichneumon
canadensis, 665
sp., 665
Ichneumonidae, 197, 566, 571, 572
Idiogaster, 827, 832
assmuthi, 832
coatoni, 832
escherichi, 832
Insect respiration, manometric calibration of, 697
Insects, numbers of, as affected by inbreeding and crossbreeding, 686
Introduced pine sawfly (see Diprion similis)
Ips pini, 542
Isopoda, ecology of, 68
Isoptera, 717
Ixodes festai, 453, 455
Ixodidae, 448, 457
Ixodoidea, 445, 457, 611, 625, 743

Japygidae of North America, 137
Johnsonomyia, 306

Korlan, against eye gnats, 537
Kronomyia, 306

Laccophilus, 424
coccinelloides, 422
insignis, 422, 424
pictus, 422
Lachnus salignus, 199
Laelaspis georgiae, 698
Lagriidae, ecology of, 72
Laphygma frugiperda, 781
Laphystia in North America, 328
(?) albiceps, 331
sabulicola, 328
Laphystia, confusa group, 329
confusa, 334
lanhami, 337
rubra, 341
rufofasciata, 342
Laphystia, flavipes group, 329
annulata, 331
brookmani, 332
cazieri, 334
flavipes, 335
snowi, 343
torpida, 344
Laphystia, howlandi group, 329
howlandi, 335
utahensis, 345
Laphystia, *jamesi* group, 329
duncani, 334
jamesi, 336
sonora, 343
Laphystia, martini group, 329
martini, 338
Laphystia, notata group, 329
bromleyi, 331
canadensis, 332
notata, 340
ochreifrons, 340
varipes, 345
Laphystia, opaca group, 329
laguna, 336
litoralis, 338
opaca, 341
texensis, 344
Laphystia, rufiventris group, 329
rufiventris, 341
Laphystia, sexfasciata group, 329
limatula, 337
sexfasciata, 342
tolandi, 344
Laphystia, species groups of
confusa, 329
flavipes, 329
howlandi, 329
jamesi, 329
martini, 329
notata, 329
opaca, 329
rufiventris, 329
sexfasciata, 329
Lardoglyphus sp., 549
Larvae of three American Cryptolestes, 8
Lauxaniidae, 134
Leeuwenhoekia (Leeuwenhoekia)
vercammeni, 183
Lepidoptera, 69, 94, 351, 474, 551, 560, 661, 726, 774, 848, 849
Lepiselaga crassipes, 3
Leptinotarsa decemlineata, 499, 502
Leptosyna, 305, 313
Leptosynini, 313
Leptothorax
ambiguus, 848
larvae, 109, 110
Leptus sp., 848
Lestremiinae, 305
Leucophaea maderae, 80, 492
Leucophenga, 133
Leucospis sp., parasite in nests of bees, 818
Leucotabanus exaestuans, 6
Ligyrocoris diffusus, 318
Linopodes
antennaepes, 67
sp., 77
Liomyrmex, larvae, 110
Liothrips tridentatus, 69
Liriomyza pictella, intraspecific competition studies of, 130
Loboptera decipiens, 80
Locustana, embryonic cuticle and glands, 538
Lonchaea sp., 73
Lonchaeidae, ecology of, 73
Lumbricus
rubellus, 553
terrestris, 553
Lyctus planicollis, biology of, 285
Lygaeidae, feeding habits, 317
Lygaeus kalmii, 319
Lygocerus, 159
sp., 405
Lygus lineolaris, effect of temperature on development, 691
Lymnaea (Stagnicola) palustris, 197
Lypha setifacies, 97

Macromischa, larvae, 109
Macromischoides, larvae, 109
Macrosiphina, 735
Macrosiphum pisi, 200
Madremyia saundersii, parasite of Choristoneura fumiferana, 97
Pseudaletia unipuncta, 665
Malaconothrus, 252
Malathion, against eye gnats, 537
Malcinae, 319
Mantodea, 720
Marietta, 384
Mastotermes darwinensis, 718
Mealworm (see Tenebrio molitor)
Mecoptera, 716, 721
Megaloblatta, 718
Megalomyrmex, larvae, 109
Megalonotinae, 317, 320
ecology of, 318
Cleradini, 320
Megalonotus chiragra, 318
Megaselia sp., 97

Meinertomyia (see Brephometra)
Melandryidae, ecology of, 72
Melanoplus
alpinus, 436
biliturates, 514
bivitattus, 200, 516
borealis, 436
bruneri, 436
food-plant preferences, 437
femur-rubrum, 518
sp., 514
Melanoplus differentialis differentialis, abnormal, 441
Melina, 192
Meloidae, 818
Merope tuber, 721
Merothrips morgani, 69
Mesochorus sp.
hyperparasite of Enypia, 566
parasite of Pseudaletia unipuncta, 665
Mesoleius tenthredinis, 476
Mesoleptus
declivus, 197
sp., 197
Mesoplophora, 251
Mesostruma, larvae, 109
Messor, larvae, 109
Metaphycus
lounsburyi, 384
luteolus, 384
biological habits, 385
sp., 384
Meteorus
communis, 665
sp., 566, 848
Method (s)
analyzing egg shells of Drosophila, 171, 732
assaying gustatory stimulant of Protoparce sexta, 499
assaying pupation sites of Drosophila melanogaster, 176
assaying sex attractant in Diprion similis, 511
calculating catch level of insects in light trap sampling, 524
collecting and rearing inhabitants of woody shelf fungi, 62
collecting and studying immature black flies, Wisconsin, 386
colorimetric, for measuring esterase activity in flies, 360, 363
comparing haemocytes of Pectinophora gossypiella, 682
comparing nutritive value of diets for Apis mellifera, 618
determining blood cell counts of Prodenia eridania, 352
determining cholinesterase and aliesterase activity in Musca domestica, 360
determining comparative survival values in house fly nutrition, 126
determining effects of chemicals and plant extracts on Pyrausta nubilalis feeding, 207
determing effects of diet and mating on Aedes aegypti, 278
determining effects of dissolved oxygen levels of flooding media on hatching of aedine mosquito eggs, 689
determining effects of exposure to radiation on Tribolium castaneum, 584
determining effect of light on temperature preferendum of Epilachna varivestis, 591
determining effects of Myzus persicae on sugars in tobacco, 221
determining effects of soil temperature and moisture on vertical distribution of Amphimallon majalis, 666
determining effects of submergence on cocoons of Pristiphora erichsonii and Mesoleius tenthredinis, 476
determining egg production and mortality of parasitized grasshoppers, 518
determining host-plant resistance to Pyrausta nubilalis, 756
determining increase of pea aphids on treated broad beans, 201
determining influence of photoperiod on oviposition by Chorizagrotis auxiliaris, 474
determining inositol requirement of Periplaneta americana, 92
determining nucleic acid content of cockroach spp., 491
determining oxygen consumption during postembryonic development of Pyrrhocoris apterus, 608
determining relationship between parental age and life cycle of Tenebrio molitor, 595
determining sex of nymphal Blattella germanica, 550
determining specificity of Protoparce sexta to host plants, 504
determining utilization of 1-C^{14}-acetate by Musca domestica, 128
determining utilization of 4-C^{14}-cholesterol by Musca domestica, 260
determining utilization of sperm by Tribolium castaneum, 557
determining vitamin content of royal jelly from honey bee colonies, 695
discriminating between pupae of Tribolium castaneum and T. confusum, 281
examining mites of Cunaxidae, 322
identifying eggs of floodwater mosquitoes, 12
inbreeding and crossbreeding insects, to test effect on fluctuations of their population, 686
intraspecific competition studies of Liriomyza pictella, 130
investigating excretory mechanism and determining pH of residual food in hindgut of beetles, 632
laminating moth wings and larvae, 847
mass-rearing of Trichoplusia ni, 229
measuring egg-laying capacity of Heterostylum robustum, 429
observing calcium oxalate crystals in oöthecae of cockroaches, 79
preparing egg shells of Drosophila for analysis, 170
preparing synthetic diets to test effect of cholesterol on Musca domestica, 821
preventing mating of Diprion similis, 511
rearing Aedes aegypti, 88
rearing cactiphilic Culicoides from field-collected cactus material, 660
rearing Drosophila melanogaster, 175
rearing Hyalomma aegyptium, 457
rearing Lyctus planicollis, 285
rearing megalonotines on seed and herbaceous materials, 318
rearing Pacific Coast aphid parasites, 404
rearing Pollenia rudis, 553
rearing Pseudaletia unipuncta, 661
rearing Scaphytopius acutus, 844
rearing Tyroglyphid mites on Neurospora, 549
recording of foregut activity in larvae of Galleria mellonella, 346
separating amino acids of seminal plasma and sperm of Apis mellifera, 841
separating amino sugars in Drosophila egg shells, 732
studying alimentary canal of Anopheles quadrimaculatus larvae, 459
studying behavior of ground-nesting bees by techniques employing plaster of Paris or Bio-plastic, 679
studying brain of abnormal Melanoplus differentialis, 441
studying Celtis bud-gall formation, 272
studying development of various stages of Lygus lineolaris, 691
studying diapause in egg of high-altitude grasshoppers, 436
studying free amino acids and carbohydrates of Pectinophora gossypiella, 439
studying heart structure of Blattella germanica, 369
studying internal development of Praon palitans, 145
studying nutritional aspects of insect respiration with manometric apparatus, 697
studying Pachypsylla celtidisgemma life cycle, 265
substituting Penicillium chrysogenum colonies for Pyrausta nubilalis, in corn-resistance assays, 758
testing baits and chemical attractants against eye gnats, 529, 835, 839
testing provisional embryonic cuticles of Dysdercus cingulatus, 538
testing respiration rate in pupae of Prodenia eridania, 849
testing transmission of bean yellow mosaic virus by Myzus persicae, 521
using plastic paint as marker for studying mites, 698
Miastor
americana, 305
metraloas, 305, 312
Miastorini, 311
Microbisium confusum, 67
Micrococcus sp., virus affecting Trichoplusia ni, 234
Microentomoninae, 675
Microgaster auripes, 665
Micromyini, 312
Microparsus, the genus, 735
desmodiorum, 736
olivei, 740
variabilis, 742
Microplitis sp., 665
Milichiella eye gnats, baits and chemical attractants against, 534
Milichiella lacteipennis, attractancy of proteinaceous preparations, 838

Milkweed bug (see Oncopeltus fasciatus)
Millotoca, 826
Miridae, 691
Mites
Caminella peraphora, 27, 28
Oribatid ecology, aspects of, 251
predatory (Cunaxidae) on citrus, 321
Tyroglyphid, rearing on Neurospora, 549
use of plastic paint as marker in studies of, 698
water, Piona, 35
Moehnia erema, 309
Monodontomerus dentipes, 849
Monomorium, larvae, 109
antarticum, 109
spp., 109
Monotomidae, ecology of, 70
Morphology of
Aedes hendersoni and A. hendersoni complex, 600
Aedes triseriatus, 601
Anopheles quadrimaculatus larval alimentary canal, 459
Anthonomus grandis, 548
A. grandis thurberiae, 548
Blattaria, pleurosternal region of, 717
Celtis galls, 265
Coleoptera, pleurosternal region of, 726
Dermaptera, mesothorax of, 720
Diptera, pterothorax of, 721
Dysdercus cingulatus, 539
Embioptera, pleurosternal region of, 718
Enypia spp., 560
Ephemeroptera, pleurosternal region of, 729
Evalljapyx, 137
excretory mechanism of stored-grain beetles, 634
Furcifera, 160
Hemiptera, pleurosternal region of, 728
Hymenoptera, pleurosternal region of, 722
immature stages of Atrichomelina pubera, 197
Isoptera, pleurosternal region of, 718
Japygidae, 137
Lepidoptera, pleurosternal region of, 726
Lyctus planicollis, 285
males of Drosophilidae, 133
Mantodea, mesothorax of, 720
Mecoptera, pleurosternal region of, 721
Neuroptera, pleurosternal region of, 721
Odonata, pleurosternal region of, 729
Orthoptera, pleurosternal region of, 721
pharyngeal gland development of Apis mellifera, 619
Plecoptera, pleurosternal region of, 717
pleurosternal region of the pterothorax, 712
Praon palitans, 144
reproductive systems in Noctuidae, 763
Rhytidoponera metallica, 793
Sciomyzinae, 197
sternum in insects, 713
Tetanocerinae, 197
Tipulidae, 198
Tribolium castaneum, 280
T. confusum, 280
Trichoptera, pleurosternal region of, 724
ultrastructure of heart of Blattella, 369
Zoraptera, pterothorax of, 720
Mosquitoes, eggs of floodwater Aedes, 11
Moth wings and larvae, laminating of, 847
Musca
cerasi, 253
cardui, 254
umbellatarum, 254
Musca domestica
cholinesterase and ali-esterase activity in organophosphorus-susceptible and -resistant strains, 360
effect of dietary cholesterol on reproduction of, 821
nutrition, 125
utilization of 1–C^{14}–acetate in lipid synthesis by adults, 128
utilization of 4–C^{14}–cholesterol, 260
Muscidae, 134
Muscina
assimilis, 665
stabulans, 96
Mycetophagidae, ecology of, 71
Mycetophagus flexuosus, 71
Mycophila, 305
Mycromyini, 305, 312
Myodocha serripes, 318
Myrafant, larvae, 109
Myrmecina, larvae, 110
Myrmica, larvae, 109
Myrmicaria, larvae, 109
Myrmicinae, ant larvae of, 98
Myrmicocrypta, larvae, 109
Myzus persicae
aphid-virus relationships, 521
effect on sugars found in tobacco, 220
honeydew of, 220
Myzus solani, abnormalities in, 708

Nasutitermes, 825
costalis, 830
kaudernianus, 830
Nauphoeta cinerea, 80, 492
Necrophlebia, 306
Nematoda, ecology of, 66
Nematophora, 572
Nemorilla pyste, 97
Neohaplusia, 306
Neorhynchocephalus sackenii, 513
major factor in decline of Melanoplus bilituratus, 515
parasitization by larvae of, 516
Neoschöngastia
americana, 190
dalmati, 191
Neostylopyga rhombifolia, 80
Neoxylocopa surinamensis, 814
Neriidae, 659
Nesomyrmex, larvae, 110
Netelia sp., 665
Neuroptera, 716, 721, 848
Nitidulidae, ecology of, 70
Noctuidae, 551, 474, 661, 763
Nomadopsis, host of Heterostylum anthidius, 426
scutellaris, 426
Nomia, host of Heterostylum, 425
melanderi, 425
behavioral studies, 679
parasites and range of, 425
triangulifera, 426
Nothrus, 252
Novomessor, larvae, 109
Nucleic acids in cockroaches, 491
Nyctibora sp., 80

Obituaries:
Barber, Harry Gardner, 853
Barnes, Horace F., 854
Bonhag, Philip Frederic, 282
Edwards, George A., 547
Octolasium lacteum, 553
Octotemnus sp., 70
Odonata, 439, 716, 729, 851
Odontacarus, 184
bakeri, 184
mastigophorus, 184
Odontoloxozus, 659
Oecacta, subgenus (see Culicoides)
Oedaspinae, 671
Oedaspis, 671
Ogcodes sp., parasites of spiders, 416
Oideprosoma, 826
Oligotoma japonica, 720
Oligotrophini, 306
Oligomyrmex, larvae, 109
Omalus in North America, 235
(Omalus) aeneus, 238
(Pseudomalus) auratus, 241
(Omalus) *butleri*, 240
(Diplorrhos) cressoni, 246
(D.) *downeyi*, 246
(Omalus) glomeratus, 240
(Diplorrhos) *granti*, 247
(D.) intermedius, 247
(Omalus) iridescens, 241
(Pseudomalus) janus, 242
(Diplorrhos) *krombeini*, 247
(Pseudomalus) *macswaini*, 244
(Diplorrhos) plicatus, 236, 435
(D.) seminudus, 248
(D.) speculum, 248
(D.) *telfordi*, 249
(Pseudomalus) *tribolatus*, 245
(Diplorrhos) variatus, 249
Omalus subgenera
Diplorrhos, 245
Omalus, 238
Pseudomalus, 236, 241
Omania, 495
coleoptrata, 496
marksae, 496
samoensis, 495
Omotoma fumiferanae, 97
Oncopeltus, 609
fasciatus, 319, 686
Oncopsis variabilis, 849
Ontholestes cingulatus, 70
Oppia, 252
Orectognathus, larvae, 109
Orellia
occidentalis, 254
occidentalis=straminea, 254
palposa, 254
ruficauda, 254
Oreodytes, sp. cf. scitulus, 422
Oribatula, 252
Oribatid mites, ecology, 251
Ornithodoros
erraticus, 454
foleyi, 446, 455

savignyi, 447, 455
tholozani, 448, 455
Orthetrum albistylum speciosum, territorialism and residentiality in, 851
Orthoptera, 441, 721
Oryzaephilus surinamensis, 70
Ozodiceromyia, 161
Ozophora picturata, 318

Pachybrachius
bilobatus, 317
vinctus, 317
Pachyneuron siphonophorae, 405
Pachypsylla celtidis-gemma
hackberry gall formation by, 272
life cycle of, 265
Paedalgus, larvae, 109
Paedogenesis, 305
Paedogenic gall midges, new classification of, 305
Pamphantinae, 319
Panchlora nivea, 80
Panorpa sp., 721
Paracoblatta
uhleriana, 80
virginica, 80
Paracacoxenus guttatus, 358
Paracorotoca, 828
Paracryptocerus, larvae, 109
Paramyrmica, larvae, 109
Parasinella, 481, (see Sinella)
Parasites
attacking Saissetia oleae, 384
California, aphid hosts of, 412
internal, of Therioaphis maculata, 144
of grasshoppers, 294, 513
of Nomia melanderi and other bees, 425
of Wisconsin black fly spp., 392, 397
insect, fish, and nematode predators, 392, 396
mermithoid nematodes, 392, 403
protozoans, microsporidian, 396, 403
sporozoans, 401
reared from Atrichomelina pubera, 197
tick, of tortoise and other fauna in Turkey, 457
Parasites (Aphidiinae), California, and their aphid hosts, 404
aphid, Pacific Coast, 405
primary parasites, 405
secondary parasites, 405
Paraterellia, 121
superba, 123
varipennis, 122, 254
ypsilon, 124, 205
Parathion, against eye gnats, 537
Paratrombium (=Parathrombium), 293
Paromius, 317
Parwinnertzia, 305
Passaloecus, host of Omalus, 235
Pea aphids, increase on treated broad beans, 199
Pectinophora gossypiella
free amino acids and carbohydrates of, 439
haemocytes of larvae and pupae, 682
Peloribates, 251
Pemphredon (Cemonus), 235
Penicillium chrysogenum colonies, substituted for borer larvae in corn-resistance assays, 758
Pentatrichopus spp., 783
brevipilosus=P. minor, 783
fragaefolii, 783
jacobi, 789
minor, 790
potentillae, 783
tetrahodus, 783
thomasi, 787
Perasis, 329
Perates insessus, 187
Peridroma margaritosa
morphology of reproductive system, 763
percentage of mating, 779
Perigenes constrictus, 318
Periplaneta
americana, 80
dietary inositol requirement, 91
australasia, 80
brunnea, 80
fuliginosa, 80
Peripsocus
madidus, 849
sp., 848
Peritrechus sp., 318
Pero (see Brephometra)
Phaenicia sericata, 665
Phaeogenes hebrus, 665
Phaeotabanus
fervens, 5
obscuripilis, 6
prasiniventris, 5
Phassus excrescens, 726
Pheidole, larvae, 109
Pheidologeton, larva, 109
Pherbellia, 192
griseola, 197
nana, 197
Philoctetes, 236
Phobocampe sp., 566
Pholeomyia, 136
Phoridae, 197
Phorocera incrassata, 97
Phortica, 136
Phostex, against eye gnats, 536
Phryxe pecosensis, 97, 665
Phycitidae, 768
Phycus, 161
Phygadeuon sp., 197
Phyrrhocoris, apterus, oxygen consumption during post-embryonic development, 606
Physiology of Aedine mosquito eggs, hatching of, 688
Phytophaga destructor, 761
Pine sawfly (see Diprion similis)
Pink bollworm (see Pectinophora gossypiella)
Piona
brunsoni, 42
carnea, 48
clavicornis, 51
coccinea americana, 38
conglobata, 49
conglobatella, 50
constricta, 51
coronis, 44
crassa, 49
debilis, 55
exilis, 46
flatheadensis, 57
floridana, 58
haberba, 56
inconstans, 57
interrupta, 35
linguaplax, 60
loda, 56
michiganensis, 40
mitchelli, 54
neumani, 50
pinguipalpis, 52
pugilis, 46
rotunda, 55
socialis, 57
spangleri, 60
spinulosa, 56
triangularis, 44
turgida, 36
uncata, 40
variabilis, 54
washingtonensis, 38
wolcotti, 48
Pionidae, 35
Piophilidae, 197
Platyzosteria novae-saelandiae, 80
Plecoptera, 716, 717, 718
Plodia sp., 770
Plutella maculipennis, 203
Podomyrma, larvae, 110
Poeciloderas quadripunctata, 6
Pogonomyrmex, larvae, 109
Polistes
annularis, 111
exclamans exclamans, 111
fuscatus fuscatus, 111
fuscatus pallipes, 111
hunteri hunteri, 111
metricus, 111
rubiginosus, 111
Pollenia rudis
feeding and development of, 553
parasite of Pseudaletia unipuncta, 665
Polyaspidae, 30
Polyporaceae, 61
Porricondylini (Epidoscini), 306
Porthetria, 608
dispar, 686
Praon
occidentalis, 410
palitans, 144, 150, 410
simulans, 148, 411
unicus, 411
volucre, 150
Predators
of Wisconsin black flies (see Parasites)
on termites, 294
Prionoxystus robinae, 726
Pristiphora erichsonii, effects of cocoon submergence, 476
Pristomyrmex, larvae, 110
Procecidochares, 671, 674
anthracina, 672
atra, 672
grindeliae, 672
Procecidocharoides, 671
caliginosa, 674
flavissima, 672
penelope, 672
pullata, 671, 673
Prodenia eridania
blood cell counts, 351
lack of elevated respiration in injured pupae, 849
Projapygidae, in North America, 575
Projapyx, 575, 582
brasiliensis, 575
congruens, 576
eburneus, 576
imperfectus, 576
incomprehensus, 576
jeanneli, 576
stylifer, 576
Promethes elongatus, 665

Prosimulium, 386
(Helodon) decemarticulatum, 394
(H.) gibsoni, 395
(Prosimulium) hirtipes complex, 392, 395
(P.) magnum, 397
sp. #1 and sp. #2, 398
Prospaltella, 702
Protentomonidae, 675
Protermitobia
comes, 833
kirbyi, 833
rhodesiae, 833
Protodejeania hystricosa, 566
Protoparce sexta
gustatory stimulant from solanaceous plants, 499
specificity to solanaceous plants, 503
Protura, new family of, 675
Pselaphochernes parvus, 67
Pseudachorutes lunatus, 68
Pseudaletia unipuncta
life history studies, 661
morphology of reproductive system, 763
percentage of mating, 779
Pseudococcus citriculus, control by Clausenia purpurea, 705
Pseudomalus, 236, 241
Pseudoperichaeta erecta, 97
Pseudoschöngastia
audyi, 191
guatemalensis, 191
Pseudoscorpionida, ecology of, 67
Pseudotritia
ardua, 252
loricata, 252
Psilocephala, 160
Psilocurus, 329
Psyllidae, 265
Pterocallidium, 145
Pteromalidae, 197, 405
Pteromicra inermis, 197
Pteronarcys, 716
Pterothorax, pleurosternal region of insects, morphology of, 712
evolution of in various insects, 716
homologies among orders of insects, 717
Ptiliidae, ecology of, 71
Pycnoscelus surinamensis, 80
Pyrausta nubilalis and its principal host plant, 206, 755
host resistance, as related to larval feeding behavior, growth and survival, 206, 755
Resistance Factors A and C, effect on larvae, 206
Pyrrhocoridae, 538

Radiation effects on Tribolium castaneum, 584
Resistance Factor A, 6-methoxybenzoxazolinone, 206
Resistance, host-plant to Pyrausta nubilalis, 206
Reticulitermes, 828
Rhabdophaga, 306
Rhabdura, suborder, 575
Rhagoletis cingulata, 671
Rhantus
atricolor, 423
mexicanus, 424
Rhipicephalus s. sanguineus, 453, 455
Rhodnius, 609
Rhopalomastix, larvae, 110
Rhytidoponera
convexa, 793
metallica, the anatomy of, 793
parasites in thorax, 808
Rogas
sp., 572
terminalis, 665
Ropalophorus, 542
clavicornis, 543
wisconsinensis, 543
Saissetia
hemispherica, 385
oleae, races and parasites of, 383
Saldidae, 494
Sarcophaga
aldrichi, 97
cooleyi, 97
Sarcophagidae, 197
Sarepta sareptana, 329
Scaphidiidae, ecology of, 69
Scaphytopius acutus, seasonal history and rearing of, 843
Scaptomyza, 133
Scarabaeidae, 72, 666
Schedorhinotermes lamanianus, 834
Scheloribates pallidula, 251
Schizelythron, 828, 833
Sciomyzidae, 192
Sciomyzinae, 197
Scolopostethus diffidens, 318
Scutellista cyanea, 384
Scydmaenidae, ecology of, 69
Seed bugs
feeding habits, 317
suggested name for Lygaeidae, 320
Selasoma tibiale, 3
Sepedon caerulea, 193
Serratia marcescens, virus affecting Trichoplusia ni, 234
Sialis, 716
Silphidae, ecology of, 69
Simuliidae, 134, 386
new North American Species (see Cnephia)
Simulium
(Gnus) corbis, 400
(Simulium) decorum, 401
(S.) jenningsi, 401
(S.) luggeri, 396, 401
(Byssodon) meridionale, 400
(B.) rugglesi, 400
venustum complex, 401
tuberosum, 393, 401
venustum, 392, 401
verecundum, 401
(Neosimulium) vittatum, 387, 392, 402
Sinella in nearctic caves, 481
alata, 486
avita, 484
barri, 488
basidens, 490
caeca, 482
cavernarum, 484
curviseta, 482
hoffmani, 488
krekeleri, 490
lucifuga, 486
Sinophthalmus pictus, 136
Siphlonurus, 716
columbianus, 729
Sisamnes clavigera, 318
Sitona cylindricollis, 696
Sitophilus granarius, 632
Slaterellinae, 319
Sminthurides
malmgreni, 68
pumilis, 68
Sminthurinus
quadrimaculatus, 68
viridis, 67
Smithistruma, larvae, 109
Snails, hosts of Sciomyzidae, 192
Solenopsis, larvae, 109
Spalangia sp., 197
Sphragisticus nebulosus, 318
Spirachtha, 825
Spirachthodes, 828
madecassus, 830
Staphylinidae
ecology of, 69
new termitophilous, 825
Staphylinus maculosus, 69
Stegana, 133
Steganinae, 133
Stenamma, larvae, 109
Stenotabanus, 365
cribellum, 365
currani, 365
guttatulus, 365
(S.) maculifrons, 6
(Aegialomyia) tobagensis, 6
Sternit modification in Drosophilidae, 133
Stabasoma
flaviventre *pulla*, 5
fulvohirtum, 4, 368
mallophoroides, 5
Stigmus, host of Omalus, 235
Stiletto-flies (see Furcifera)
Strawberry aphid complex, 783
Strawberry-virus vectors (see Pentatrichopus spp.)
Strobliellini, 308
Strumigenys, larvae, 109
Stygnocoris
rusticus, 318
pedestris, 318
Styporrhamphis, 366
Sugars found in tobacco as affected by Myzus persicae, 220
Suprella supellectilium, 80
Symphylurinus, 575, 582
almeidai, 575, 582
arléi, 575
blanguernoni, 576, 582
discretus, 575, 582
grassii, 575, 582
indicus, 576
lutzi, 575
marcuzzii, 575, 582
occidentalis, 576
orientalis, 576
paratus, 575, 582
perceptus, 576
peregrinus, 575
simplex, 575
stangei, 580, 583, 824
swani, 576
travassosi, 575
tristanii, 575
Syrphidae, 659

Tabanidae
new North American, notes on catalog of Nearctic spp., 364
of Trinidad, 1
unrecognizable spp., 368
Tabanus
atratus, 366
americanus, 366
basivitta, 7
bellardii, 368

claripennis, 6
colombensis, 7
commixtus, 7
confligens, 7
discifer, 7
importunus, 7
johannesi, 8
lineola
carneus (var.), 7
hinellus (var.), 366
plangens (var.), 367
nebulosus, 7
nigripes, 366
olivaceiventris, 7
pseudoculus, 6
pungens, 6
sorbillans, 6
trivittatus, 8
vittiger
caymanicus, 368
guatemalanus, 7, 367
schwardti, 365
unrecognizable spp., 368
winthemi, 366
xipe, 6
Tachinidae, 476, 572
Taxonomy, importance of to biological control, 701
Tecomatlana sandovali, 187
Tectocepheus velatus, 252
Tenebrio
embryonic cuticle and glands, 538
molitor, relationship between parental age and life cycle, 595
Tenebrionidae, 280, 584
Tenthredinidae, 476
Tenuiala, 252
Tephritidae, 253, 671
new genus of, 121
Termitana, 826
Termites, predators on, 294
Termitochara, 826
Termitogastrina, 826
Termitomimus, 826
Termitona congoensis, 833, 834
Termitophya, 827
Termitoptochus, 827
australiensis, 832
Termitoptocinus, 826
Termitopullus, 826
Tetanocerinae, 197
Tetramorium, larvae, 109
Tettigonia pulchella, 18
Thereva, 161
Therevidae, 160
Therioaphis
maculata, 144
biological control of, 404
riehmi, 159
trifolii, 145, 159
Thermonectus, marmoratus, 422
Thoracophorus costalis, 69
Thurberia weevil (see Anthonomus grandis thurberiae)
Thyreoxenus, 826
brevitibialis, 830
mexicanus, 830
Thysanoptera, 68, 507
Thysanura, 714
Thysanus, 384
Tibicen bifida, 728
Tick, tortoise, host relationships, 457
Ticks of Lybia, 445
biology, 445
disease relationships, 445
distribution, 445
ecology, 445
hosts, 445
Tipulidae, 198
Tobacco, sugars found in, as affected by Myzus persicae, 220
Tortricidae, 94
Toxoptera graminum, 761
Tracheoniscus rathkei, 68
Trachymyrmex, larvae, 109
Trachyrhachis kiowa, 514
Trachysphyrus albitarsis, 665
Trachytidae, 27
Trachytinae, 31
Trap, light, for sampling activity and abundance, 524
Tribolium
castaneum, sperm precedence in fertilization of eggs, 557
postirradiation feeding activity of, 584
confusum, 263, 632
recognition of pupae, 280
Tribolium, discrimination between pupae of T. castaneum and T. confusum, 280
Trichoplusia ni, mass-rearing of, 229
diseases of, 234
failure to increase on treated cabbages, 203
Trichopseniinae, 828, 833
Trichopsidea clausa, 513
Trichoptera, 717, 724
Trichopteromyia, 306
Triclis argentifacies, 329
Trigonoderus unguttus, 64, 72
Trigonogaster, larvae, 110
Trinervitermes, 826, 828
Trioxys
(Acanthocaudus) schlingeri, 411
(Trioxys) sp., 412
(T.) utilis, 144, 158, 411
Trombicula
(Eutrombicula) alfreddugesi, 187
(E.) batatas, 188
(Leptotrombidium) panamensis *hamaxiaia*, 188
Trombiculidae, 183
Trombidiidae, 293
Tropisternus
collaris, 424
mexicanus mexicanus, 424
Trypeta, 253
angustigena, 258
artemisiae, 253
atra, 671
flaveola, 259
fractura, 258
inaequalis, 259
maculosa, 257
penelope, 671
sigma, 256
tortile, 256
varipennis, 121
Trypoxylon, host of Omalus, 235
Tumulitermes, 828
Typhaea stercorea, 71
Typhlocyba sp., 849
Typhlodromus sp., 848

Veliidae, 729
Veromessor, larvae, 109
Vespidae, 111
Vinegar flies (see fruit flies)
Virus, bean yellow mosaic, transmission by Myzus persicae, 521
Vollenhovia, larvae, 110

Wasmannia, larvae, 109
Whartonia
nudosetosa, 185
womersleyi, 185
Winnertzia, 305
Winthemia
rufopicta, 665
sp., prob. militaris, 665

Xenogaster, 828
Xenomyrmex, larvae, 109
Xestocis levettei?, 67, 71
Xestocoris nitens, 318
Xyela sp., 724
Xylocelia, host of Omalus, 235
Xylocopa, 809
artifex, type species of *Stenoxylocopa*, 809, 814
nesting habits, 819
(*Stenoxylocopa*) *nogueirai*, 814
nesting habits, 816
parasites in nests, 818
surinamensis, 809
Xylocopini, 809

Zabrops, 329
Zele sp., 566, 572
Zeridoneus, 319
Zoraptera, 720
Zygoribatula, 252, 848

ANNALS
OF THE
ENTOMOLOGICAL SOCIETY
OF AMERICA

Published by the

ENTOMOLOGICAL SOCIETY OF AMERICA

Volume 53 — 1960

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Published by the

ENTOMOLOGICAL SOCIETY OF AMERICA

R. H. NELSON, *Executive Secretary*
4603 Calvert Road,
College Park, Maryland

ROLAND F. HUSSEY, *Editor*
Department of Biology
University of Florida,
Gainesville, Florida

F. W. POOS, *Managing Editor*
4603 Calvert Road
College Park, Maryland

EDITORIAL BOARD

L. E. ROSEBOOM, *Chairman*, Baltimore, Md. (D, 1960)
J. A. ADAMS, Poughkeepsie, N. Y. (C, 1961)
J. J. PRATT, Wayland, Mass. (B, 1962)
F. N. YOUNG, Bloomington, Ind. (A, 1963)
P. D. HURD, Berkeley, Calif. (A, 1964)

ENTOMOLOGICAL SOCIETY OF AMERICA

OFFICERS FOR 1960

President—M. P. JONES, Washington, D. C.

President-elect—H. M. HARRIS, Ames, Iowa

Executive Secretary—R. H. NELSON, 4603 Calvert Road, College Park, Maryland

GOVERNING BOARD*

M. P. JONES, Washington, D. C. (1961)

J. E. BUSSART, Chicago, Ill. (North Central, 1960)

ROY HANSBERRY, Modesto, Calif. (F, 1961)

D. R. LINDSAY, Bethesda, Md. (D, 1962)

E. G. LINSLEY, Berkeley, Calif. (A, 1960)

C. M. MEADOWS, Waco, Tex. (Southwestern, 1961)

R. H. NELSON, College Park, Md. (non-voting)

L. D. NEWSOM, Baton Rouge, La. (Southeastern, 1962)

P. W. OMAN, Beltsville, Md. (1960)

C. B. PHILIP, Hamilton, Mont. (Pacific, 1962)

MORRIS ROCKSTEIN, New York, N. Y. (B, 1960)

R. W. SHERMAN, Washington, D. C. (E, 1962)

E. A. STEINHAUS, Berkeley, Calif. (C, 1961)

NEELY TURNER, New Haven, Conn. (Eastern, 1961)

*Section or Branch represented and year term expires shown in parentheses.

TABLE OF CONTENTS—VOLUME 53

ADAMS, J. A., see D. H. PALMITER (Nov.) 843
AINSCOUGH, B. D., see G. W. KRANTZ (Jan.) 27
AITKEN, T. H. G., see G. B. FAIRCHILD (Jan.) 1
ANDERSON, JOHN R., AND ROBERT J. DICKE—Ecology of the Immature Stages of Some Wisconsin Black Flies (Simuliidae: Diptera) (May) 386

BARON, R. L., AND F. E. GUTHRIE—A Quantitative and Qualitative Study of Sugars Found in Tobacco as Affected by the Green Peach Aphid, *Myzus persicae*, and Its Honeydew (March) 220
BARTLETT, BLAIR R.—Biological Races of the Black Scale, *Saissetia oleae*, and Their Specific Parasites (May) 383
BEARD, RAIMON L.—Electrographic Recording of Foregut Activity in Larvae of *Galleria mellonella* (May) 346
BECK, STANLEY D.—The European Corn Borer, *Pyrausta nubilalis*, and Its Principal Host Plant. VII. Larval Feeding Behavior and Host Plant Resistance (March) 206
BECK, STANLEY D., AND EDWARD E. SMISSMAN—The European Corn Borer, *Pyrausta nubilalis*, and Its Principal Host Plant. VIII. Laboratory Evaluation of Host Resistance to Larval Growth and Survival (Nov.) 755
BECK, STANLEY D., see ROGER HOOPINGARNER (Sci. Note, Sept.) 697
BERG, C. O., see B. A. FOOTE (March) 192
BIGLEY, WALTER S., AND FREDERICK W. PLAPP, Jr.—Cholinesterase and Ali-Esterase Activity in Organophosphorus-Susceptible and -Resistant House Flies (May) 360
BISHOP, GUY W.—Taxonomic Observations on the Larvae of the Three American *Cryptolestes* (Coleoptera: Cucujidae) That Infest Stored Grain (Jan.) 8
BLUM, M. S., see A. F. NOVAK (Nov.) 841
BOHART, G. E., W. P. STEPHEN AND R. K. EPPLEY—The Biology of *Heterostylum robustum* (Diptera: Bombyliidae), a Parasite of the Alkali Bee (May) 425
BOHART, R. M.—Addendum to a Review of the Genus *Omalus* Panzer in North America (Hymenoptera, Chrysididae) (May) 435
BOHART, R. M., AND L. E. CAMPOS—A Review of the Genus *Omalus* Panzer in North America (Hymenoptera, Chrysididae) (March) 235
BRELAND, OSMOND P.—Restoration of the Name, *Aedes hendersoni* Cockerell, and Its Elevation to Full Specific Rank (Diptera: Culicidae) (Sept.) 600
BRENNAN, JAMES M., AND HERBERT C. DALMAT—Chiggers of Guatemala (Acarina: Trombiculidae) (March) 183

CALLAHAN, PHILIP S., AND JOAN BEGGS CHAPIN—Morphology of the Reproductive Systems and Mating in Two Representative Members of the Family Noctuidae, *Pseudaletia unipuncta* and *Peridroma margaritosa*, with Comparison to *Heliothis zea* (Nov.) 763
CAMPOS, L. E., see R. M. BOHART (March) 235
CASIDA, J. E., see H. C. COPPEL (July) 510
CHADBOURNE, DANVILLE S., see EDGAR W. CLARK (Sept.) 682
CHALLICE, CYRIL E., see GEORGE A. EDWARDS (May) 369
CHAPIN, JOAN BEGGS, see PHILIP S. CALLAHAN (Nov.) 763
CHAPMAN, H. C.—Observations on *Aedes melanimon* and *A. dorsalis* in Nevada (Nov.) 706
CHRISTIANSEN, K.—The Genus *Sinella* Brook (Collembola: Entomobryidae) in Nearctic Caves (July) 481
CLARK, EDGAR W.—A Comparative Study of the Free Amino Acids and Carbohydrates of the Pink Bollworm, *Pectinophora gossypiella* (Sci. Note, May) 439
CLARK, EDGAR W., AND DANVILLE S. CHADBOURNE—The Haemocytes of Nondiapause and Diapause Larvae and Pupae of the Pink Bollworm (Sept.) 682
COCHRAN, D. G., see MARY H. ROSS (Sci. Note, July) 550
COLE, FRANK R.—Stiletto-Flies of the Genus *Furcifera* Kröber (Diptera: Therevidae) (March) 160
CONRAD, MARLIN S.—Laminating Moth Wings and Larvae (Sci. Note, Nov.) 847
COOK, DAVID R.—Water Mites of the Genus *Piona* in the United States (Acarina: Pionidae) (Jan.) 35
COPPEL, HARRY C.—Empty Cocoons of the Introduced Pine Sawfly, *Diprion similis*, as Habitat Niches for Arthropods (Sci. Note, Nov.) 847
COPPEL, HARRY C.—Key to the Adults of the Dipterous Parasites of the Spruce Budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) (Jan.) 94
COPPEL, H. C., J. E. CASIDA, AND W. C. DAUTERMAN—Evidence for a Potent Sex Attractant in the Introduced Pine Sawfly, *Diprion similis* (Hymenoptera: Diprionidae) (July) 510
COXETER, W. J., see D. H. PALMITER (Nov.) 843
CRAIG, GEORGE B., JR., AND WILLIAM R. HORSFALL—Eggs of Floodwater Mosquitoes. VII. Species of *Aedes* Common in the Southeastern United States (Diptera: Culicidae) (Jan.) 11

DALMAT, HERBERT C., see JAMES M. BRENNAN (March) 183
DAUTERMAN, W. C., see H. C. COPPEL (July) 510
DEBACH, PAUL—The Importance of Taxonomy to Biological Control as Illustrated by the Cryptic History of *Aphytis holoxanthus* n. sp. (Hymenoptera: Aphelinidae), a Parasite of *Chrysomphalus aonidum*, and *Aphytis coheni* n. sp., a Parasite of *Aonidella aurantii* (Nov.) 701
DEFOLIART, G. R., AND B. V. PETERSON—New North American Simuliidae of the Genus *Cnephia* Enderlein (Diptera) (March) 213
DELONG, D. M., see J. N. LILES (March) 277
DICKE, ROBERT J., see JOHN R. ANDERSON (May) 386
DORNER, ROBERT W., see MIR S. MULLA (July) 529
DORNER, ROBERT W., see MIR S. MULLA (Nov.) 835

EDWARDS, GEORGE A., AND CYRIL E. CHALLICE—The Ultrastructure of the Heart of the Cockroach, *Blattella germanica* (May) 369
EHRLICH, PAUL R., see ROBERT R. SOKAL (March) 174
EPPLEY, R. K., see G. E. BOHART (May) 425
EPSTEIN, BENJAMIN, see DAVID PIMENTEL (Sci. Note, July) 553
ERIKSEN, CLYDE H.—The Oviposition of *Enallagma exsulans* (Odonata: Agrionidae) (Sci. Note, May) 439
EVANS, DAVID—A Revision of the Genus *Enypia* (Lepidoptera: Geometridae) (Sept.) 560

FAIRCHILD, G. B., AND T. H. G. AITKEN—Additions to the Tabanidae (Diptera) of Trinidad, B.W.I. (Jan.) 1
FIORE, CARL, see DANIEL LUDWIG (Sept.) 595
FOOTE, B. A., S. E. NEFF AND C. O. BERG—Biology and Immature Stages of *Atrichomelina pubera* (Diptera: Sciomyzidae) (March) 192
FOOTE, RICHARD H.—A New North American Fruit Fly Genus, *Procecidocharoides* (Diptera: Tephritidae) (Sept.) 671
FOOTE, RICHARD H.—HORACE F. BARNES, 1902–1960 (Obituary, Nov.) 854

FOOTE, RICHARD H.—*Paraterellia*, a New Genus of Tephritidae from the Western United States (Diptera) (Jan.) ... 121
FOOTE, RICHARD H.—The Genus *Trypeta* Meigen in American North of Mexico (Diptera: Tephritidae) (March) ... 253
FORGASH, ANDREW J., AND RAYMOND F. MOORE—Dietary Inositol Requirement of *Periplaneta americana* (Jan.) ... 91
FRAENKEL, G. S., see ROBERT T. YAMAMOTO (July) ... 499
FRAENKEL, G. S., see ROBERT T. YAMAMOTO (July) ... 503

GARBER, M. J., see MIR S. MULLA (July) ... 529
GEORGHIOU, GEORGE P., see MIR S. MULLA (July) ... 529
GEORGHIOU, GEORGE P., see MIR S. MULLA (Nov.) ... 835
GORZ, H. J., see W. L. HOWE (Sci. Note, Sept.) ... 696
GRAVES, ROBERT C.—Ecological Observations on the Insects and Other Inhabitants of Woody Shelf Fungi (Basidiomycetes: Polyporaceae) in the Chicago Area (Jan.) ... 61
GREENBERG, BERNARD—House Fly Nutrition. II. Comparative Survival Values of Sucrose and Water (Jan.) ... 125
GUPTA, P. D., AND R. N. SINHA—Excretion and Its Products in Some Stored-Grain-Infesting Beetles (Sept.) ... 632
GUTHRIE, F. E., see R. L. BARON (March) ... 220
GYRISCO, GEORGE G., see R. L. RIDGWAY (Sept.) ... 691
GYRISCO, GEORGE G., see H. H. SHOREY (Sept.) ... 666

HALL, JACK C., see EVERT I. SCHLINGER (March) ... 144
HALL, JACK C., see EVERT I. SCHLINGER (May) ... 404
HARDY, D. ELMO, AND MARSHALL R. WHEELER—*Paracacoxenus*, New Genus, with Notes on *Cacoxenus indagator* Loew (Diptera: Drosophilidae) (May) ... 356
HARWOOD, ROBERT F., see RICHARD C. MAXWELL (March) ... 199
HAYDAK, MYKOLA H.—Vitamin Content of Royal Jelly from Honey Bee Colonies Fed Normal Diet and from Those Fed Pollen Substitutes (Sci. Note, Sept.) ... 695
HERON, R. J.—The Relative Effects of Cocoon Submergence on the Mortality of the Larch Sawfly, *Pristiphora erichsonii* (Hymenoptera: Tenthredinidae) and Its Parasite *Bessa harveyi* (Diptera: Tachinidae) (July) ... 476
HERVEY, G. E. R., see F. L. MCEWEN (March) ... 229
HILCHEY, J. D., see W. I. ROGERS (Sept.) ... 584
HIND, ALFRED T., see EDWIN W. KING (July) ... 524
HO, FRANK K.—Discrimination Between the Pupae of *Tribolium confusum* Duv. and *T. castaneum* (Hbst.) (Coleoptera: Tenebrionidae) (Sci. Note, March) ... 280
HOOGSTRAAL, HARRY, AND MAKRAM N. KAISER—Observations on Ticks (Ixodoidea) of Libya (July) ... 445
HOOGSTRAAL, HARRY, AND MAKRAM N. KAISER—Some Host Relationships of the Tortoise Tick, *Hyalomma* (*Hyalommasta*) *aegyptium* (L.) (Ixodoidea, Ixodidae) in Turkey (July) ... 457
HOOGSTRAAL, HARRY, AND GLEN M. KOHLS—Observations on the Subgenus *Argas* (Ixodoidea, Argasidae, Argas). 1. Study of *A. reflexus reflexus* (Fabricius, 1794), the European Bird Argasid (Sept.) ... 611
HOOGSTRAAL, HARRY, AND GLEN M. KOHLS—Observations on the Subgenus *Argas* (Ixodoidea, Argasidae, *Argas*). 3. A Biological and Systematic Study of *A. reflexus hermanni* Audouin, 1827 (Revalidated), the African Bird Argasid (Nov.) ... 743
HOOGSTRAAL, HARRY, see GLEN M. KOHLS (Sept.) ... 625
HOOPINGARNER, ROGER, AND STANLEY D. BECK—Manometric Calibration for Insect Respiration (Sci. Note, Sept.) ... 697
HORSFALL, WILLIAM R., see GEORGE B. CRAIG, JR. (Jan.) ... 11
HOWE, W. L., AND H. J. GORZ—Feeding Preferences of the Cowpea Aphid Among Species of *Melilotus* (Sci. Note, Sept.) ... 696
HOWELL, J. FRANKLIN—A Technique Employing Bio-Plastic in the Excavation of Burrows of Ground-Nesting Bees (Sept.) ... 679
HUBERT, A. A., see W. W. WIRTH (Sept.) ... 639
HUNTER, PRESTON E.—Plastic Paint as a Marker for Mites (Sci. Note, Sept.) ... 698
HUNTER, PRESTON E., see ROBERT R. SOKAL (March) ... 174
HURD, PAUL D., JR., AND J. S. MOURE—A New World Subgenus of Bamboo-Nesting Carpenter Bees Belonging to the genus *Xylocopa* Latreille (Hymenoptera: Apoidea) (Nov.) ... 809

ITO, YOSIAKI—Territorialism and Residentiality in a Dragonfly, *Orthetrum albistylum speciosum* (Odonata: Anisoptera) (Sci. Note, Nov.) ... 851

JACOBSON, L. A.—Influence of Photoperiod on Oviposition by the Army Cutworm *Chorizagrotis auxiliaris*, (Lepidoptera: Noctuidae), in an Insectary (July) ... 474
JONES, JACK COLVARD—The Anatomy and Rhythmical Activities of the Alimentary Canal of *Anopheles* Larvae (July) ... 459
JONES, JACK COLVARD, see CHARLES R. ROSENBERGER—(May) ... 351
JUDSON, CHARLES L.—The Physiology of Hatching of Aedine Mosquito Eggs: Hatching Stimulus (Sept.) ... 688

KAISER, MAKRAM N., see HARRY HOOGSTRAAL (July) ... 445
KAISER, MAKRAM N., see HARRY HOOGSTRAAL (July) ... 457
KAPLANIS, J. N., W. E. ROBBINS, AND L. A. TABOR—The Utilization and Metabolism of 4-C^{14}-Cholesterol by the Adult House Fly (March) ... 260
KAPLANIS, J. N., see W. E. ROBBINS (Sci. Note, Jan.) ... 128
KELLEN, W. R.—A New Species of *Omania* from Samoa, with Notes on Its Biology (Heteroptera: Saldidae) (July) ... 494
KEMMERER, A. R., see L. N. STANDIFER (Sept.) ... 618
KING, ABRAM, see BARBARA STAY (Jan.) ... 79
KING, EDWIN W., AND ALFRED T. HIND—Activity and Abundance in Insect Light Trap Sampling (July) ... 524
KING, EDWIN W., AND ROBERT C. RILEY—Effect of Light on the Temperature Preferendum of Larvae of the Mexican Bean Beetle, *Epilachna varivestis* (Sept.) ... 591
KOHLS, GLEN M., AND HARRY HOOGSTRAAL—Observations on the Subgenus *Argas* (Ixodoidea, Argasidae, *Argas*). 2. *A. cooleyi*, New Species, from Western North American Birds (Sept.) ... 625
KOHLS, GLEN M., see HARRY HOOGSTRAAL (Sept.) ... 611
KOHLS, GLEN M., see HARRY HOOGSTRAAL (Nov.) ... 743
KRANTZ, G. W., AND B. D. AINSCOUGH—*Caminella peraphora*, a New Genus and Species of Mite from Oregon (Acarina: Trachytidae) (Jan.) ... 27
KREASKY, JOSEPH B.—Extended Diapause in Eggs of High-Altitude Species of Grasshoppers, and a Note on Food-Plant Preferences of *Melanoplus bruneri* (May) ... 436

LAMBREMONT, EDWARD N.—Postemergence Changes of Enzyme Activity in the Mosquito *Aedes aegypti* (L.) (Jan.) ... 86
LEONARD, MORTIMER D., AND REECE I. SAILER—HARRY GARDNER BARBER, 1871–1960 (Obituary, Nov.) ... 853
LILES, J. N., AND D. M. DELONG—The Longevity and Productivity of Adult Male and Female *Aedes aegypti* When Reared Separately and Together on Three Different Diets (March) ... 277
LINSLEY, E. G., AND RAY F. SMITH—PHILIP FREDERIC BONHAG, 1923–1959 (Obituary, March) ... 282
LIUZZO, J. A., see A. F. NOVAK (Nov.) ... 841
LOULOUDES, S. J., see W. E. ROBBINS (Sci. Note, Jan.) ... 128

LUDWIG, DANIEL, AND CARL FIORE—Further Studies on the Relationship Between Parental Age and the Life Cycle of the Mealworm, *Tenebrio molitor* (Sept.) ... 595

MATSUDA, RYUICHI—Morphology of the Pleurosternal Region of the Pterothorax in Insects (Nov.) ... 712
MAXWELL, RICHARD C., AND ROBERT F. HARWOOD—Increased Reproduction of Pea Aphids on Broad Beans Treated with 2,4-D (March) ... 199
MCCAUGHEY, W. F., see L. N. STANDIFER (Sept.) ... 618
MCEWEN, F. L., AND G. E. R. HERVEY—Mass-Rearing the Cabbage Looper, *Trichoplusia ni*, with Notes on Its Biology in the Laboratory (March) ... 229
MECCA, CHRISTYNA E.—Lack of Elevated Respiration in Injured Pupae of the Southern Armyworm, *Prodenia eridania* (Lepidoptera) (Sci. Note, Nov.) ... 849
MEDLER, J. T.—*Agrosoma*, a New Genus for *Tettigonia pulchella* Guérin and Related Species (Homoptera: Cicadellidae) (Jan.) ... 18
MITLIN, NORMAN—Determination of Nucleic Acids in the Testes of Three Cockroach Species (July) ... 491
MONROE, R. E.—Effect of Dietary Cholesterol on House Fly Reproduction (Nov.) ... 821
MONROE, R. E., see W. E. ROBBINS (Sci. Note, Jan.) ... 128
MOORE, RAYMOND F., see ANDREW J. FORGASH (Jan.) ... 91
MOURE, J. S., see PAUL D. HURD, JR. (Nov.) ... 809
MULLA, MIR S., ROBERT W. DORNER, GEORGE P. GEORGHIOU AND M. J. GARBER—Olfactometer and Procedure for Testing Baits and Chemical Attractants Against *Hippelates* Eye Gnats (July) ... 529
MULLA, MIR S., GEORGE P. GEORGHIOU AND ROBERT W. DORNER—Effect of Aging and Concentration on the Attractancy of Proteinaceous Materials to *Hippelates* Gnats (Nov.) ... 835
MUMA, MARTIN H.—Predatory Mites of the Family Cunaxidae Associated with Citrus in Florida (May) ... 321

NEFF, S. E., see B. A. FOOTE (March) ... 192
NEUNZIG, H. H.—The Pupae of *Heliothis zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) (Sci. Note, July) ... 551
NEWELL, IRWIN M., AND LLOYD TEVIS, JR.—*Angelothrombium pandorae* N. G., N. Sp. (Acari, Trombidiidae), and Notes on the Biology of the Giant Red Velvet Mites (May) ... 293
NOVAK, A. F., M. S. BLUM, S. Taber, III, AND J. A. LIUZZO—Separation and Determination of Seminal Plasma and Sperm Amino Acids of the Honey Bee, *Apis mellifera* (Nov.) ... 841

OATMAN, EARL R.—Intraspecific Competition Studies of the Melon Leaf Miner, *Liriomyza pictella* (Thomson) (Diptera: Agromyzidae) (Sci. Note, Jan.) ... 130
O'NEILL, KELLIE—Identification of the Newly Introduced Phlaeothripid, *Haplothrips ?clarisetis* Priesner (Thysanoptera) (July) ... 507

PALMITER, D. H., W. J. COXETER AND J. A. ADAMS—Seasonal History and Rearing of *Scaphytopius acutus* (Homoptera: Cicadellidae) (Nov.) ... 843
PETERSON, B. V., see G. R. DEFOLIART (March) ... 213
PHILIP, CORNELIUS B.—New North American Tabanidae. XI. Supplemental Notes Pertinent to a Catalog of Nearctic Species (May) ... 364
PIMENTEL, DAVID, AND BENJAMIN EPSTEIN—The Cluster Fly, *Pollenia rudis* (Diptera: Calliphoridae) (Sci. Note, July) ... 553
PIMENTEL, DAVID, MAURICE W. RUMSEY AND FREDERICK A. STREAMS—Rearing Tyroglyphid Mites on *Neurospora* (Sci. Note, July) ... 549
PLAPP, FREDERICK W., JR., see WALTER S. BIGLEY (May) ... 360
POND, D. D.—Life History Studies of the Armyworm, *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), in New Brunswick (Sept.) ... 661
PRESCOTT, HUBERT W.—Suppression of Grasshoppers by Nemestrinid Parasites (Diptera) (July) ... 513
PRICE, DOUGLAS W.—A New Family of Protura from California (Sept.) ... 675
PRITCHARD, A. EARL—A New Classification of the Paedogenic Gall Midges Formerly Assigned to the Subfamily Heteropeziinae (Diptera: Cecidomyiidae) (May) ... 305

RABB, R. L.—Biological Studies of *Polistes* in North Carolina (Hymenoptera: Vespidae) (Jan.) ... 111
RIDGWAY, R. L., AND GEORGE G. GYRISCO—Effect of Temperature on the Rate of Development of *Lygus lineolaris* (Hemiptera: Miridae) (Sept.) ... 691
RILEY, ROBERT C., see EDWIN W. KING (Sept.) ... 591
ROBBINS, W. E., J. N. KAPLANIS, S. J. LOULOUDES AND R. E. MONROE—Utilization of 1-C^{14}-Acetate in Lipid Synthesis by Adult House Flies (Sci. Note, Jan.) ... 128
ROBBINS, W. E., see J. N. KAPLANIS (March) ... 260
ROGERS, W. I., AND J. D. HILCHEY—Studies on Postirradiation Feeding Activity of *Tribolium castaneum* (Tenebrionidae: Coleoptera) (Sept.) ... 584
ROSENBERGER, CHARLES R., AND JACK COLVARD JONES—Studies on Total Blood Cell Counts of the Southern Armyworm Larva, *Prodenia eridania* (Lepidoptera) (May) ... 351
ROSS, MARY H., AND D. G. COCHRAN—A Simple Method for Sexing Nymphal German Cockroaches (Sci. Note, July) ... 550
ROTH, LOUIS M., see BARBARA STAY (Jan.) ... 79
RUMSEY, MAURICE W., see DAVID PIMENTEL (Sci. Note, July) ... 549
RUSSELL, LOUISE M.—Notes on the Entomological Writings of ASA FITCH, M.D., with Special Reference to his Catalogues and Reports (May) ... 326
RYCKMAN, RAYMOND E.—Biology of Cactiphilic Species of Ceratopogonidae (Diptera) (Sept.) ... 659

SAHNI, S. L., see R. K. SHARAN (July) ... 538
SAILER, REECE I., see MORTIMER D. LEONARD (Obituary, Nov.) ... 853
SCHAEFERS, G. A.—A Systematic Study on the Strawberry Aphid Complex (*Pentatrichopus* spp.) (Nov.) ... 783
SCHLAGER, GUNTHER—Sperm Precedence in the Fertilization of Eggs in *Tribolium castaneum* (Sept.) ... 557
SCHLAGER, GUNTHER, see ROBERT R. SOKAL (March) ... 174
SCHLINGER, EVERT I.—A Review of the Genus *Eulonchus* Gerstaecker, Part I. The Species of the *smaragdinus* Group (Diptera: Acroceridae) (May) ... 416
SCHLINGER, EVERT I., AND JACK C. HALL—Biological Notes on Pacific Coast Aphid Parasites, and Lists of California Parasites (Aphidiinae) and Their Aphid Hosts (Hymenoptera: Braconidae) (May) ... 404
SCHLINGER, EVERT I., AND JACK C. HALL—The Biology, Behavior, and Morphology of *Praon palitans* Muesebeck, an Internal Parasite of the Spotted Alfalfa Aphid, *Therioaphis maculata* (Buckton) (Hymenoptera: Braconidae, Aphidiinae) (March) ... 144
SEEVERS, CHARLES H.—New Termitophilous Staphylinidae of Zoogeographic Significance (Coleoptera) (Nov.) ... 825
SHANDS, W. A., see H. E. WAVE (Nov.) ... 708
SHARAN, R. K., AND S. L. SAHNI—Provisional Embryonic Cuticles of *Dysdercus cingulatus* (Hemiptera: Pyrrhocoridae) (July) ... 538
SHENEFELT, ROY D.—*Ropalophorus* Haliday—A Genus New to North America (Hymenoptera: Braconidae: Euphorinae) (July) ... 542

SHOREY, H. H., AND GEORGE G. GYRISCO—Effects of Soil Temperature and Moisture on the Vertical Distribution of European Chafer Larvae (Sept.)... 666
SIMPSON, G. W., see H. E. WAVE (Nov.)..... 708
SINHA, R. N., see P. D. GUPTA (Sept.)..... 632
SLÁMA, KAREL—Oxygen Consumption During the Postembryonic Development of *Pyrrhocoris apterus* (Heterometabola: Heteroptera), and Its Comparison with That of Holometabola (Sept.)..... 606
SLIFER, ELEANOR H.—An Abnormal Grasshopper With Two Median Ocelli (Orthoptera, Acrididae) (Sci. Note, May)..... 441
SMISSMAN, EDWARD E., see STANLEY D. BECK (Nov.). 755
SMITH, CLYDE F., AND NAZIFE TUATAY—The Genus *Microparsus* Patch (Aphidae: Homoptera) (Nov.). 735
SMITH, LESLIE M.—Japygidae of North America, 5. Species of *Evalljapyx* with 30±1 Segments in the Antenna (Order Diplura) (March)..... 137
SMITH, LESLIE M.—The Families Projapygidae and Anajapygidae (Diplura) in North America (Sept.). 575
SMITH, RAY F., see E. G. LINSLEY (Obituary, March). 282
SOKAL, ROBERT R., PAUL R. EHRLICH, PRESTON E. HUNTER AND GUNTHER SCHLAGER—Some Factors Affecting Pupation Site of *Drosophila* (March)..... 174
STANDIFER, L. N., W. F. MCCAUGHEY, F. E. TODD AND A. R. KEMMERER—Relative Availability of Various Proteins to the Honey Bee (Sept.)..... 618
STAY, BARBARA, ABRAM KING AND LOUIS M. ROTH—Calcium Oxalate in the Oothecae of Cockroaches (Jan.)..... 79
STEPHEN, W. P., see G. E. BOHART (May)..... 425
STREAMS, FREDERICK A., see DAVID PIMENTEL (Sci. Note, July)..... 549
SWEET, MERRILL H.—The Seed Bugs: A Contribution to the Feeding Habits of the Lygaeidae (Hemiptera: Heteroptera) (May)..... 317
SWENSON, K. G.—Aphid-Virus Relationships in the Transmission of Bean Yellow Mosaic Virus by *Myzus persicae* (July)..... 521

TABER, S., III, see A. F. NOVAK (Nov.)..... 841
TABOR, L. A., see J. N. KAPLANIS (March)..... 260
TEVIS, LLOYD, JR., see IRWIN M. NEWELL (May).... 293
TODD, F. E., see L. N. STANDIFER (Sept.)..... 618
TOMKINS, VICTOR N.—GEORGE A. EDWARDS, 1914–1960 (Obituary, July)..... 547
TUATAY, NAZIFE, see CLYDE F. SMITH (Nov.)..... 735
TURNER, NEELY—The Effect of Inbreeding and Crossbreeding on Numbers of Insects (Sept.)..... 686

WALTON, B. C. JAMES—The Life Cycle of the Hackberry Gall-Former, *Pachypsylla celtidis-gemma* (Homoptera: Psyllidae) (March)..... 265
WAVE, H. E., W. A. SHANDS AND G. W. SIMPSON—Some Abnormalities in the Foxglove Aphid in Northeastern Maine (Nov.)..... 708
WERNER, FLOYD G.—A New Character for the Identification of the Boll Weevil and the Thurberia Weevil (Coleoptera: Curculionidae) (Sci. Note, July)..... 548
WHEELER, GEORGE C., AND JEANETTE WHEELER—The Ant Larvae of the Subfamily Myrmicinae (Jan.)..... 98
WHEELER, JEANETTE, see GEORGE C. WHEELER (Jan.)..... 98
WHEELER, MARSHALL R.—Sternite Modification in Males of the Drosophilidae (Diptera) (March)..... 133
WHEELER, MARSHALL R., see D. ELMO HARDY (May)..... 356
WHELDEN, ROY M.—The Anatomy of *Rhytidoponera metallica* F. Smith (Hymenoptera: Formicidae) (Nov.)..... 793
WILCOX, J.—*Laphystia* Loew in North America (Diptera: Asilidae) (May)..... 328
WILSON, B. R.—Some Chemical Components of the Egg Shell of *Drosophila melanogaster*. I. Amino Acids (March)..... 170
WILSON, B. R.—Some Chemical Components of Egg Shell. II. Amino Sugars and Elements (Nov.).. 732
WIRTH, W. W., AND A. A. HUBERT—Ceratopogonidae (Diptera) Reared From Cacti, With a Review of the *Copiosus* Group of *Culicoides* (Sept.)..... 639
WOOLLEY, TYLER A.—Some Interesting Aspects of Oribatid Ecology (Acarina) (March)..... 251
WRIGHT, C. G.—Biology of the Southern Lyctus Beetle, *Lyctus planicollis* (May)..... 285

YAMAMOTO, ROBERT T., AND G. S. FRAENKEL—Assay of the Principal Gustatory Stimulant for the Tobacco Hornworm, *Protoparce sexta*, from Solanaceous Plants (July)..... 499
YAMAMOTO, ROBERT T., AND G. S. FRAENKEL—The Specificity of the Tobacco Hornworm, *Protoparce sexta*, to Solanaceous Plants (July)..... 503
YOUNG, FRANK N.—The Colors of Desert Water Beetles—Environmental Effect or Protective Coloration? (May)..... 42

WINNING COMBINATION IN EVERY DROP

No insecticide has yet approached malathion's combination of powerful, wide-range insect control and low toxicity to man and animals.

One drop of malathion is all it takes to kill 300,000 aphids . . . yet *you* don't need a respirator or special protective clothing to handle it safely.

For fruit and vegetables, malathion offers control of most major insect pests. It can be used close to harvest *without* residue problems . . . up to 1 day on some crops, three days on most crops.

For fruit, malathion offers powerful insect control with safety for finish of sensitive apple varieties.

Write for MALATHION GROWER'S GUIDE PE-5039: American Cyanamid Company, Agricultural Division, 30 Rockefeller Plaza, New York 20, N. Y.

CYANAMID
MALATHION
INSECTICIDES

CYANAMID SERVES THE MAN WHO MAKES A BUSINESS OF AGRICULTURE

VELSICOL

INSECTICIDES

Versatility and lasting residual action have made them useful throughout the world for control of insects that attack homes and gardens, damage crops, and carry disease.

HEPTACHLOR

...for soil insect control in agriculture!

In hundreds of soil insect control tests conducted since its introduction, Heptachlor has proven to be a most efficient soil insecticide for use on corn and other major crops.

ENDRIN

...for hard to kill pests of major crops!

Endrin is relatively new, but 1960 saw the development of many new uses for this powerful, versatile insecticide. Apples, potatoes, cotton and other crops were extensively treated with Endrin during the past year.

CHLORDANE

...for termite, public health, household, lawn and garden insect control!

Chlordane continues to be a most popular insecticide with pest control operators and homeowners. It has an excellent safety and performance record.

TECHNICAL INFORMATION AVAILABLE ON REQUEST FROM

VELSICOL CHEMICAL CORPORATION

330 East Grand Avenue, Chicago 11, Illinois

Velsicol International Corporation, C.A., P.O. Box 1587 — Nassau, Bahamas, B.W.I.

Miscellaneous Publications

of the ENTOMOLOGICAL SOCIETY OF AMERICA

This new periodical contains timely and scholarly articles of 20 printed pages or more. The individual numbers appear at irregular intervals. Each volume will contain about 200 pages.

VOLUME 1, NUMBER 1, pp. 1–32 appeared October 1, 1959, and contains the symposium papers on Insecticide Resistance in Arthropods of Medical and Veterinary Importance given at the Salt Lake City meeting in December 1958. Authors are H. F. Schoof, R. B. March, A. W. A. Brown, and Herbert Knutson.

VOLUME 1, NUMBER 2, pp. 33–68 appeared February 17, 1960 and contains a "Phylogenetic-Systematic Study of Larval Oedemeridae (Coleoptera)" by Jerome G. Rozen, Jr.

VOLUME 1, NUMBER 3, pp. 69–171 appeared July 27, 1960 and contains the following: "Swarming and Mating in Mosquitoes," by Erik Tetens Nielsen and James S. Haeger. "A Revision of the Genus *Chlaenius* Bonelli (Coleoptera, Carabidae) in North America," by Ross T. Bell.

Prices for NUMBERS 1 and 2 of VOLUME 1

Single copy	$2.50 each
2–24 copies	$2.25 each
25–99 copies	$2.00 each
100—or more copies	$1.50 each

Prices for NUMBER 3 of VOLUME 1

Single copy	$6.00 each
2–24 copies	$5.50 each
25–99 copies	$5.00 each
100—or more copies	$4.00 each

VOLUME 2, NUMBER 1, pp. 1–175 contains the papers presented on the Symposium—Research Progress on Insect Resistance held in Washington, D. C., October 7 and 8, 1959 (Issued October 19, 1960.)

Prices for NUMBER 1 of VOLUME 2

Single copy	$7.50 each
2–24 copies	$6.75 each
25–99 copies	$6.00 each
100—or more copies	$5.00 each

TERMS OF SUBSCRIPTION. $10.00 per volume in North America and U. S. Possessions, $10.50 elsewhere. Deliveries overseas are not guaranteed and foreign mailings are made at the subscriber's risk.

ENTOMOLOGICAL SOCIETY OF AMERICA

4603 Calvert Road, College Park, Maryland

TABLE OF CONTENTS

PAGE

DeBach, Paul—The Importance of Taxonomy to Biological Control as Illustrated by the Cryptic History of *Aphytis holoxanthus* n. sp. (Hymenoptera: Aphelinidae), a Parasite of *Chrysomphalus aonidum*, and *Aphytis coheni* n. sp., a Parasite of *Aonidiella aurantii*..... 701

Chapman, H. C.—Observations on *Aedes melanimon* and *A. dorsalis* in Nevada..... 706

Wave, H. E., W. A. Shands and G. W. Simpson—Some Abnormalities in the Foxglove Aphid in Northeastern Maine..... 708

Matsuda, Ryuichi—Morphology of the Pleurosternal Region of the Pterothorax in Insects.. 712

Wilson, B. R.—Some Chemical Components of *Drosophila melanogaster* Egg Shell. II. Amino Sugars and Elements..... 732

Smith, Clyde F., and Nazife Tuatay—The Genus *Microparsus* Patch (Aphidae: Homoptera)..... 735

Hoogstraal, Harry and Glen M. Kohls—Observations on the Subgenus *Argas* (Ixodoidea, Argasidae, *Argas*). 3. A Biological and Systematic Study of *A. reflexus hermanni* Audouin, 1827 (Revalidated), the African Bird Argasid..... 743

Beck, Stanley D., and Edward E. Smissman—The European Corn Borer, *Pyrausta nubilalis*, and its Principal Host Plant. VIII. Laboratory Evaluation of Host Resistance to Larval Growth and Survival..... 755

Callahan, Philip S. and Joan Beggs Chapin—Morphology of the Reproductive Systems and Mating in Two Representative Members of the Family Noctuidae, *Pseudaletia unipuncta* and *Peridroma margaritosa*, with Comparison to *Heliothis zea*..... 763

Schaefers, G. A.—A Systematic Study on the Strawberry Aphid Complex (*Pentatrichopus* spp.)..... 783

Whelden, Roy M.—The Anatomy of *Rhytidoponera metallica* F. Smith (Hymenoptera: Formicidae)..... 793

Hurd, Paul D., Jr., and J. S. Moure—A New-World Subgenus of Bamboo-Nesting Carpenter Bees Belonging to the Genus *Xylocopa* Latreille (Hymenoptera: Apoidea)..... 809

Monroe, R. E.—Effect of Dietary Cholesterol on House Fly Reproduction..... 821

Seevers, Charles H.—New Termitophilous Staphylinidae of Zoogeographic Significance (Coleoptera)..... 825

Mulla, Mir S., George P. Georghiou and Robert W. Dorner—Effect of Aging and Concentration on the Attractancy of Proteinaceous Materials to *Hippelates* Gnats..... 835

Novak, A. F., M. S. Blum, S. Taber, III and J. A. Liuzzo—Separation and Determination of Seminal Plasma and Sperm Amino Acids of the Honey Bee, *Apis mellifera*..... 841

Palmiter, D. H., W. J. Coxeter and J. A. Adams—Seasonal History and Rearing of *Scaphytopius acutus* (Homoptera: Cicadellidae)..... 843

Scientific Notes:

Conrad, Marlin S.—Laminating Moth Wings and Larvae..... 847

Coppel, Harry C.—Empty Cocoons of the Introduced Pine Sawfly, *Diprion similis*, as Habitat Niches for Arthropods..... 847

Mecca, Christyna E.—Lack of Elevated Respiration in Injured Pupae of the Southern Armyworm, *Prodenia eridania* (Lepidoptera)..... 849

Ito, Yosiaki—Territorialism and Residentiality in a Dragonfly, *Orthetrum albistylum speciosum* (Odonata: Anisoptera)..... 851

Obituaries:

Harry Gardner Barber, 1871–1960..... 853

Horace F. Barnes, 1902–1960..... 854

Book Reviews.....762, 808, 855

Erratum..... 824